THE AMERICAN NATURALIST

A BI-MONTHLY JOURNAL

Devoted to the Advancement and Correlation
of the Biological Sciences

CONTENTS

Date of Issue: June 16, 1961

THE AMERICAN NATURALIST is a bimonthly journal devoted to furthering the objectives of The American Society of Naturalists, which are the "discussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution, thus serving to correlate the various biological sciences into a common philosophy of biology." It will publish those general addresses, essays and papers presented at the symposia of biological societies which contribute to the above purpose; research papers and reviews in which theoretical interpretation and synthesis are predominant; and brief discussion, criticism and comment on material published in this journal and elsewhere. "Letters to the Editors" containing new information or comment will be dated when received and published in the next issue. They should not exceed two printed pages.

Manuscripts and editorial correspondence should be addressed to the Editor, Institute of Microbiology, Rutgers-The State University, New Brunswick, New Jersey.

Correspondence concerning subscriptions, advertisements, and business matters should be addressed to The American Naturalist, Box 1574, Lancaster, Pa. Remittances should be made payable to The American Naturalist.

Members of The American Society of Naturalists should correspond with the treasurer of the Society, Dr. Nelson T. Spratt, Department of Biology, University of Minnesota, Minneapolis 14, Minnesota, concerning dues and membership subscriptions.

Correspondence concerning membership and other matters pertaining to the Society should be addressed to the Secretary, Dr. Earl L. Green, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.

Subscription, $8.00 a year, postpaid in the United States, $8.50 in Canada, $8.75 elsewhere. Special rates for students, apply to the publisher. Single copies may be purchased for $1.35 for issues of the current year and $2.00 for issues after 1939; $3.00 for earlier issues.

BIG AND LITTLE POPULATIONS: AN AMATEUR'S EXCURSION*

L. C. DUNN
Columbia University, New York City

A custom of nearly eighty years in this society imposes an obligation that on one occasion each year the president shall speak and the members present shall listen. Since the speaker calls the tune, he will usually choose a topic which lies closer to his own experience than to the professional work of other members. I shall take this general course, but since I can claim no special competence in the methods, now sophisticated and mathematical, of relating the genetical structure of populations to evolutionary theory, I shall treat of big and little populations as an amateur.

The proper flavor of that word was rendered, I think, by a young man who visited me while I was, as we say, at work in the laboratory. "But," said he, after a period of observation, "do they actually pay you for doing this? And besides, it's Sunday." An amateur may work for love (even when he gets paid for it) but it is the non-professional attitude which distinguishes him. This calls for a certain naiveté, which I suspect is shared by many members of this society.

For have not most of us at times wondered what it is that makes small populations so interesting? By small, I mean first, few in numbers. Whether we judge size as census takers do by counting all individuals or as geneticists do by counting only those who contribute genes to the next generation, we find animals, plants, and men in groups of finite size, many of them very small. Living things being what they are, small groups seem to represent beginnings or endings, the germs of something bigger or the remnants of groups that now run the risk of extinction. Herein lies an appeal that is in part romantic, and the amateur on his excursion should confess that attraction to his scientific colleagues, and boast of it to other amateurs. The last of the Mohicans call to us with a stronger voice than the whole of the Five Nations, and those few who speak a disappearing language become more precious than those whose speech has conquered a wide world. The little band of animals or plants which share a new and rare mutation turns our

minds toward the future. What will come of this? Rarity to be sure gives value, but why, when markets do not enter in, should this be so? Is it that "all things counter, original, spare, strange" excite in us the admiration which is the response of our own stubborn will to be ourselves, to be unique?

For admiration is a reaction which the amateur does not suppress. I must confess that this is what I feel when thinking of the small band of Eskimos which conducts its life fully and independently in a harsh environment. I think them clever; I admire, too, the device by which they defeat the rule which some demographers have called the law of population minimum. This turns out to be a demographer's rule and not an Eskimo one. The demographers based it on monogamy, but the Eskimos by declaring a seasonal moratorium on this custom got around the difficulties of asymmetrical distributions of ages and sexes to which small human populations are subject, and survive in bands below the so-called legal minimum.

Consider, too, the small villages in which most of our forbears lived and found their mates and which still persist in many parts of the world. In the village each person is known to all the others; the individual peculiarities which make human beings interesting are likely to be more fully apparent than in the larger populations. The society is, as the anthropologists say, a "face to face" one, and this generates the drama that we savor. If the mating circle keeps itself closed behind social walls of local tradition and dialect and defensive pride, when these replace the physical walls, then it will be perforce small, and if these are long continued, the community is destined to develop sharp peculiarities within itself. Genes which seldom meet their likes in big populations come to expression when relatives marry, and contrasts between homozygotes are sharper than among the usual run of heterozygotes which always constitute the majority of people in big populations.

The small remnant of a once dominant flora which clings as a relict population to its mountain top has an inevitable attraction for the botanist; as have for the zoologist the disjunct colonies of a species occurring in small pockets over a wide range, each with its sharp local peculiarities, showing as it were the flexibility of which the whole species is capable. The achievements of a small band of house mice, which, having left the easier life of towns, establish a new community in the desert, redound to the credit of all mice everywhere. And so we think them clever too, and leave to later computation the part that luck played in survival. The mere survival of a small population like that of the European bison is a matter for wonder, assailed as it is by chance processes of many kinds. Admiration first before the bare fact, and then the questions—how do they do it, and what is its meaning for the succession of populations, for evolution?

But smallness in numbers is not the whole meaning of my title. Small may mean also the dimensions of the members. Surely it will seem more remarkable to the naive excursionist that a virus particle should harbor a microcosm of genes than that a mouse should and more remarkable for mouse

than man. Something of this sort was felt when this complexity was first revealed in the little vinegar fly which weighs a half a milligram and has 10,000 genes. Upon reflection we realize that virus, mouse, and man all have the same problem to meet, of maintaining fitness and flexibility, and that multiplicity of genes is a good way to do this. But with amateurs wonder precedes reflection.

My reason for retaining this double meaning of small is that my first excursion was with a small four-legged mammal, and my second with a bigger two-legged one. Both come in big and little populations and both can be found in all habitable parts of this globe, often sharing a common table, one under it, the other above. In each the gene pool is potentially as wide as the species, but in practice genes circulate chiefly in smaller eddies in the pool, constituting the local races of mice and of men. Sometimes the eddies are very small indeed, so that a good deal of local inbreeding occurs. Mice deal with this more openly than men and in their ignorance of Oedipus let nature take its course. But men surround their mating practices with tabus, like that against incest, and these harden into codified laws. Thus, the outcome of human reproduction is influenced by both nature and acquired culture.

Of course mice are more biddable than men, and will generally breed when you ask them to and provide suitable conditions. This fact, and their smaller size, made it possible to learn more quickly about the four-legged ones. So I should like to tell you first about them and later about some modest lessons taught by the bigger ones.

What took us first upon the mouse excursion was the discovery in long domesticated laboratory populations of a series of allelic genes with three peculiar properties. First, they were lethal in early embryonic stages; second, they were transmitted from male heterozygotes in ratios far exceeding those expected from Mendel's first rule; and, third, they gave rise to new alleles by a process resembling mutation, but occurring at a rate far above any known mutation rate. Some of the first of these mutations turned up during the war when parts of the Manhattan project were housed a few stories below our mouse room, and as soon as the mystery of the atom-smashers' operations was dispelled, we had to suffer some good-natured ribbing about the causes of our "spontaneous" mutations. So we said we would ask some more innocent mice about it, mice without university connections, living their own lives in houses or barns or out in nature. Their reply was very clear: we, too, know about such mutations; in fact, quite a lot of us already have them. The outcome of our first collections was to find that most wild house mouse populations in the U.S.A. contain heterozygotes for such genes, generally lethals, in frequencies up to about 50 per cent. Later a similar pattern was found in Japan. This posed a new problem. How could lethal genes be maintained in such high frequencies when natural selection was eliminating all mice homozygous for them? The main clue to this was revealed when it turned out that all such alleles found in wild populations (16 were studied) were transmitted from heterozygous males to over 90 per cent of their progeny. Here were two evolutionary forces

acting in opposite directions, one to reduce, the other to increase the frequencies of such genes. Which of these should prevail?

With the aid of more mathematically minded colleagues and students, we figured out what should happen to alleles subject to these two forces in large random-breeding populations. The first model, based on the usual Hardy-Weinberg assumptions of large numbers, equal mutation pressures on both alleles, and equal action of selection on the surviving genotypes, indicated that the second force—high male transmission rate of a lethal —should prevail and produce at equilibrium a condition in which 80–90 per cent of the population was heterozygous for the lethal. But we had never found a population like this. The highest frequencies found within a local population were less than 60 per cent, usually less than 50 per cent. And so we knew that real mice in nature were behaving differently from the hypothetical ones of the model.

Now one way in which natural populations always differ from those in the ideal universe of probabilities is in their size. In the latter, size is infinite, in the former it is limited. What if the natural populations were very small indeed? Could this provide conditions to counteract the great advantage of high transmission ratio and limit the frequencies of lethals to those found in nature? A critic of our first deterministic model, Professor Gert Bonnier of Stockholm, pointed out in a protracted correspondence, that in very small populations, chance alone should lead to loss of lethals and fixation of normal alleles in many of the small breeding units. Professor Richard Lewontin posed this question to the 650 digital computer at the University of Rochester. What would happen in analogue populations continuously generated by small random samples of gametes from family groups containing a few heterozygotes with lethals favored by high male transmission ratios? The answer was clear. Given time enough, such small groups of eight or fewer individuals tended to lose the lethals, and in such as did, the normal alleles got fixed. A local population under this model should thus consist of some breeding groups from which the lethal had been lost and of others still unfixed but threatened always by the same erosion of gene frequencies in one direction. Clearly, in such a system, a local population, as mice collected in one area, would be a composite of still smaller population units, the family or breeding units. A population gene frequency would be an average of the current state of the smaller units through which the lethal alleles were drifting in a state of flux, birds of passage as it were, introduced for a time by migration or mutation, eventually to be lost by chance.

Now this was no novel idea. Sewall Wright had reached this conception long before, basing upon it his fertile view of intergroup selection as providing the most favorable condition for evolutionary change. To find that it provided a reasonable model for the study of cases subjected to the extreme conditions found in our mice: that is, abnormally high transmission ratio advantage of genes against which natural selection operates so drastically is new evidence of its usefulness. It leads, to be sure, in this case, toward another extreme, for assumptions of extremely small sizes of breeding

groups are required to make it applicable, and we don't yet know to what
extent this corresponds to conditions in nature. Nor do we know what other
variables act upon the breeding groups: migrations, local habitat and selec-
tive forces, and the complex of behavior patterns associated with mating
and household formation and avoiding predators and disease and getting a
living generally. But at any rate, one amateur has learned from this excur-
sion how small a small population must be in order that chance, operating
through random drift, may interpose an effective check to the accumulation
and spread of lethals.

And so now to a brief excursion among the larger two-legged mammals,
toward the benefit of which, in the end, most learning is directed. The pros-
pects for testing, directly, on human populations, ideas derived from the
very small populations generated by mice or by machines are admittedly not
very good. But man has the irresistible attraction of being the most inter-
esting mammal of all and that lures the amateur.

Even though we were to put ourselves for the moment in the position of
mice observing men, I think we should still consider that the larger animal
presents more problems than the smaller one, hence would be more interest-
ing to the curious mouse. In a sense, I look at man from the mouse's view-
point. Although I know, as a two-legged amateur, that the essential biologi-
cal properties of all species are inherently similar, hence equally interest-
ing, still I can reflect upon the list of qualities which a literate mouse might
compile when contemplating man. At the head of the list would be the ex-
treme diversification which the commensal would observe in his host. He
would not need to (as he could not) appreciate the biological diversity which
is so apparent to us. What he would observe is the extreme degree of cul-
tural diversity, which has no parallel in other organisms. He (the mouse)
has shared the cave, the castle, and the cooperative housing project and all
the habitats in between; he has had stone pebble tools thrown at him and
has been obliterated by clean atomic bombs; he has been put through, albeit
symbolically, a digital computer and has been addressed in symbols that
range from the first spoken curse or incantation to the final code of informa-
tion theory and has even provided some of the latter through yielding up his
DNA. And from his present vantage point as he rides a circling vehicle
above this planet, he has the opportunity, could he but read the code, to
learn at the same moment that the walls of Jericho have yielded their mes-
sage of the antiquity of man's civilization, and that the digital computer is
now old-fashioned. What he cannot observe, since all his observations die
with himself, is the dimension in man which holds this all together—his
consciousness of history. It is this which, in Korszybski's quaint term,
makes man the "time-binder" for whom both past and future are connected
in the present. The concern of this bigger animal with where he goes from
here is coeval with his humanness, and as the species matures, it is in-
creasingly concerned with where it came from. In a sense all human in-
quiries, as they become meaningful, acquire historical forms.

Biological questions are inevitably colored by our experience that all
present systems are determined by past events. Questions about human

populations, whether couched in cultural or biological terms, are clear examples of this form of thought, and it is especially evident when we think of small populations. For then, to the battery of questions about microevolution which we can pose to the micro-populations of the mouse, can be added that one which is specifically human—what part has culture played?

The amateur's excursion carried him into two small human populations isolated from the bigger ones in which they are embedded by cultural barriers which had grown up over the centuries. The questions which he asked did not concern primarily the cultural differences which led to isolation and kept the populations small and endogamous; rather they had to do with the effect that isolation and small size exerted upon the biological compositions and structures of the populations. But anyone interested in human biology can no more overlook the cultural determinants of diversity than the biologist interested in animal populations can neglect the ecological milieu in which their structures take form. Culture, in fact, provides a large part of the ecology of man. And so I must say something about the forces that acted on these two small human populations.

One is a Jewish enclave within the Catholic population of Rome; the other, the descendants of Negro slaves now living on one of the Sea Islands (James Island) near Charleston, South Carolina. The chief circumstance accounting for the present state of the two to three hundred families comprising the ghetto community of Rome is the growth of the Jewish tradition and faith and the inherited tradition of marriage within it. This we can say is due to self-recognition of membership in a community based on common culture of which religion is one but not the only part. Self-identification has been reinforced by attitudes in the culture around it both as represented by Imperial Rome and by the Christian papacy which succeeded it and inherited some of the cultural traits of the pre-Christian Rome to which the ancestors of these Jews were brought from Palestine. Throughout the twenty centuries of its existence this community has been recognized as a distinct cohesive cultural unit.

The ancestors of the Negroes of James Island were brought, in the 17th or 18th century, from Africa. The designation as Gullah of the dialect formerly spoken by them seems to stem from a supposed derivation from Angola near the bulge of the west coast of Africa, but this is far from certain. Self-recognition has also played its part in maintaining some integrity in the population, but the larger part has been due to recognition by the Europeans who brought them and amongst whom they have since lived, of cultural traits and especially of biological ones which set them off as a group. Black skin is a biological difference to be sure, but the way in which it influences mating patterns constitutes an effect of culture. In other species the occurrence of a sizeable minority of melanic forms does not lead to assortative mating such as we see in human societies in which both forms occur. Human, too, is the social value attached to this character. I had the impression that, contrary to the state of affairs in the cities, amongst the island Gullahs, black has high value and may serve as reinforcement of linguistic and other cultural heritages from Africa in maintaining the biological char-

· acter of the community. And of course commercialized slavery, to which the community owed its origin in the New World, is a distinctively human institution supported by cultural sanctions.

The influence of culture on population biology is exerted chiefly through its effects on the mating pattern; for this determines the way in which genes circulate within or between human populations. Small populations are perforce endogamous, and endogamy is likely to limit population size although there are cultural ways of escaping from this, as some of the larger Indian castes have discovered.

A direct way of studying the effects of cultural factors is by counting the kinds and arrangements of genes in small communities. Most useful are the genes controlling the antigens of the red blood cells, the so-called blood group systems, which can be classified objectively and counted. Subjects must, of course, be persuaded each to give up some five cc. of blood, and for this some substitute for the trapping method employed with mice must be used. Such methods go under the general title of diplomacy, and each investigator uses those which produce the desired result. If he succeeds he gets a description of that part of the community gene pool which can be diagnosed by the antisera at his disposal. This may lead him to estimates of the frequency in the community of each of 20 or more alleles belonging to eight to ten blood group systems; and if he can test some of the hemoglobin variants, his gene frequency estimates can be greatly extended. His status as amateur gets more and more insecure as new methods of diagnosing gene differences are employed and he had better depend, as I did, on professionals in these complex fields. Fortunately, the professionals welcome the help of the amateur, for many of them have in view the same problems of human microevolution to which these descriptions of gene frequencies in small populations are ultimately addressed.

And so by collaborative work involving many persons a description of a population emerges in terms of the kinds of genes found in it. Several questions will then arise. Some refer to the community as a unit. Do the genes in a population caused to be endogamous by small size and social isolation fall into patterns of arrangement similar to those found in larger open populations in which the ratios of homozygotes and heterozygotes approach the proportions predicted by application of the Hardy-Weinberg equilibrium rule? For the common alleles which will constitute the bulk of the sample, departures from the rule can only be expected in very large gene samples derived by very close inbreeding—and in human communities these conditions are usually mutually antithetic. In common with other observers, I failed to find evidence of this effect of endogamy in the communities I sampled, although deliberately planned tests of this point in more favorable populations may give a different answer. But other smaller questions had some interesting light thrown on them. In each community certain rarer genes occurred in unexpectedly high frequency. These tended to cluster in a few family lines, as might have been expected if a rare migrant or mutant had chanced to pass his peculiar allele to descendants within the community. Similarly, chance may account for the absence or rarity, in the small community, of some

alleles which are commoner in the neighboring populations. Accident plays a larger role in determining the biological characters of small than of large populations.

But the chief use of such descriptions is comparative. Does the small population have an assortment of genes characteristic of it and different from the assortments of other related groups? This appeared to be the case for the ghetto community of Rome when compared with Catholic Italians. It was true also of the Negroes of James Island; no secure indication was found that European genes were regularly entering the community which maintains its African character in the New World. This merely states in biological terms the facts of observation that Jews marry Jews, and Africans, Africans. But it is a necessary step in the documentation of that observation and leads to further biological tests of the effects of cultural habits—whether Jews of one particular community, for example, conserve by endogamy a genetic patrimony peculiar to that community and whether this process leads to biological differentiation within the whole cultural body.

The more important comparative question can be elucidated only when gene frequency descriptions of many separated communities become available; do these have biological peculiarities in common? If they do, how much of this is attributable to historical forces which tended to maintain the integrity of a people anciently dispersed in small communities amongst populations of widely different characters? And what accounts for differences amongst the dispersed communities—selection, drift, intermarriage, mutation?

A few excursions of an amateur will not provide the observations needed to elucidate these questions. Rather, the efforts of many amateurs and professionals of various kinds including anthropologists and historians will be needed, and this is, of course, now proceeding in many parts of the world. What one learns from dealing with such questions at first hand is to recognize the real existence of the elementary units of population structure in man as in other creatures, and that these are probably small. One learns, too, respect for the stubborn conservatism with which two-legged animals cling to customs generated by social life. Human reproduction begins, so to speak, in the head; and the patterns of gene distribution are altered by extra-biological forces of great potency.

In these excursions the amateur never learned, as must now be obvious, how big is big, or how small is small. This is the great unsolved question about populations not only of mice and men but of all bisexual creatures. Theoretical analyses suggest that small populations supply essential trial-and-error testing grounds for life in big ones, but this is yet to be documented by actual estimates of numbers. What one does learn, however, is that it is genes which have to be counted, not heads or bodies, for it is these elements which constitute the essential communities, and that the bigger gene pools which have heretofore borne the name of populations have to be viewed through what is learned of the smaller eddies which endow the whole with the power of movement.

THE PARADOX OF THE PLANKTON*

G. E. HUTCHINSON

Osborn Zoological Laboratory, New Haven, Connecticut

The problem that I wish to discuss in the present contribution is raised by the very paradoxical situation of the plankton, particularly the phytoplankton, of relatively large bodies of water.

We know from laboratory experiments conducted by many workers over a long period of time (summary in Provasoli and Pintner, 1960) that most members of the phytoplankton are phototrophs, able to reproduce and build up populations in inorganic media containing a source of CO_2, inorganic nitrogen, sulphur, and phosphorus compounds and a considerable number of other elements (Na, K, Mg, Ca, Si, Fe, Mn, B, Cl, Cu, Zn, Mo, Co and V) most of which are required in small concentrations and not all of which are known to be required by all groups. In addition, a number of species are known which require one or more vitamins, namely thiamin, the cobalamines (B_{12} or related compounds), or biotin.

The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials. The problem is particularly acute because there is adequate evidence from enrichment experiments that natural waters, at least in the summer, present an environment of striking nutrient deficiency, so that competition is likely to be extremely severe.

According to the principle of *competitive exclusion* (Hardin, 1960) known by many names and developed over a long period of time by many investigators (see Rand, 1952; Udvardy, 1959; and Hardin, 1960, for historic reviews), we should expect that one species alone would outcompete all the others so that in a final equilibrium situation the assemblage would reduce to a population of a single species.

The principle of competitive exclusion has recently been under attack from a number of quarters. Since the principle can be deduced mathematically from a relatively simple series of postulates, which with the ordinary postulates of mathematics can be regarded as forming an axiom system, it follows that if the objections to the principle in any cases are valid, some or all the biological axioms introduced are in these cases incorrect. Most objections to the principle appear to imply the belief that equilibrium under a given set of environmental conditions is never in practice obtained. Since the deduction of the principle implies an equilibrium system, if such sys-

tems are rarely if ever approached, the principle though analytically true, is at first sight of little empirical interest.

The mathematical procedure for demonstrating the truth of the principle involves, in the elementary theory, abstraction from time. It does, however, provide in any given case a series of possible integral paths that the populations can follow, one relative to the other, and also paths that they cannot follow under a defined set of conditions. If the conditions change the integral paths change. Mere failure to obtain equilibrium owing to external variation in the environment does not mean that the kinds of competition described mathematically in the theory of competitive exclusion are not occuring continuously in nature.

Twenty years ago in a Naturalists' Symposium, I put (Hutchinson, 1941) forward the idea that the diversity of the phytoplankton was explicable primarily by a permanent failure to achieve equilibrium as the relevant external factors changed. I later pointed out that equilibrium would never be expected in nature whenever organisms had reproductive rates of such a kind that under constant conditions virtually complete competitive replacement of one species by another occurred in a time (t_c), of the same order, as the time (t_e) taken for a significant seasonal change in the environment. Note that in any theory involving continuity, the changes are asymptotic to complete replacement. Thus ideally we may have three classes of cases:

1. $t_c \ll t_e$, competitive exclusion at equilibrium complete before the environment changes significantly.
2. $t_c \simeq t_e$, no equilibrium achieved.
3. $t_c \gg t_e$, competitive exclusion occurring in a changing environment to the full range of which individual competitors would have to be adapted to live alone.

The first case applies to laboratory animals in controlled conditions, and conceivably to fast breeding bacteria under fairly constant conditions in nature. The second case applies to most organisms with a generation time approximately measured in days or weeks, and so may be expected to occur in the plankton and in the case of populations of multivoltine insects. The third case applies to animals with a life span of several years, such as birds and mammals.

Very slow and very fast breeders thus are likely to compete under conditions in which an approach to equilibrium is possible; organisms of intermediate rates of reproduction may not do so. This point of view was made clear in an earlier paper (Hutchinson, 1953), but the distribution of that paper was somewhat limited and it seems desirable to emphasize the matter again briefly.

It is probably no accident that the great proponents of the type of theory involved in competitive exclusion have been laboratory workers on the one hand (for example, Gause, 1934, 1935; Crombie, 1947; and by implication Nicholson, 1933, 1957) and vertebrate field zoologists (for example, Grinnell, 1904; Lack, 1954) on the other. The major critics of this type of ap-

proach, notably Andrewartha and Birch (1954), have largely worked with insects in the field, often under conditions considerably disturbed by human activity.

DISTRIBUTION OF SPECIES AND INDIVIDUALS

MacArthur (1957, 1960) has shown that by making certain reasonable assumptions as to the nature of niche diversification in homogeneously diversified[1] biotopes of large extent, the distribution of species at equilibrium follows a law such that the rth rarest species in a population of S_s species and N_s individuals may be expected to be

$$\frac{N_s}{S_s} \sum_{i=1}^{r} \frac{1}{S_s - i + 1} .$$

This distribution, which is conveniently designated as type I, holds remarkably well for birds in homogeneously diverse biotopes (MacArthur, 1957, 1960), for molluscs of the genus Conus (Kohn, 1959, 1960) and for at least one mammal population (J. Armstrong, personal communication). It does not hold for bird faunas in heterogeneously diverse biotopes, nor for diatoms settling on slides (Patrick in MacArthur, 1960) nor for the arthropods of soil (Hairston, 1959). Using Foged's (1954) data for the occurrence of planktonic diatoms in Braendegård Sø on the Danish island of Funen, it is also apparent (figure 1) that the type I distribution does not hold for such assemblages of diatom populations under quite natural conditions either.

MacArthur (1957, 1960) has deduced two other types of distribution (type II and type III) corresponding to different kinds of biological hypotheses. These distributions, unlike type I, do not imply competitive exclusion. So far in nature only type I distributions and a kind of empirical distribution which I shall designate type IV are known. The type IV distribution given by diatoms on slides, in the plankton and in the littoral of Braendegård Sø, as well as by soil arthropods, differs from the type I in having its commonest species commoner and all other species rarer. It could be explained as due to heterogeneous diversity, for if the biotope consisted of patches in each one of which the ratio of species to individuals differed, then the sum of the assemblages gives such a curve. This is essentially the same as Hairston's (1959) idea of a more structured community in the case of soil arthropods than in that of birds. It could probably arise if the environment changed in favoring temporarily a particular species at the expense of other species before equilibrium is achieved. This is, in fact, a sort of temporal analogue to

[1] A biotope is said to be *homogeneously diverse* relative to a group of organisms if the elements of the environmental mosaic relevant to the organism are small compared to the mean range of the organisms. A *heterogeneously diverse biotope* is divided into elements at least some of which are large compared to the ranges of the organisms. An area of woodland is homogeneously diverse relative to most birds, a large tract of stands of woodland in open country is heterogeneously diverse (Hutchinson, 1957, 1959).
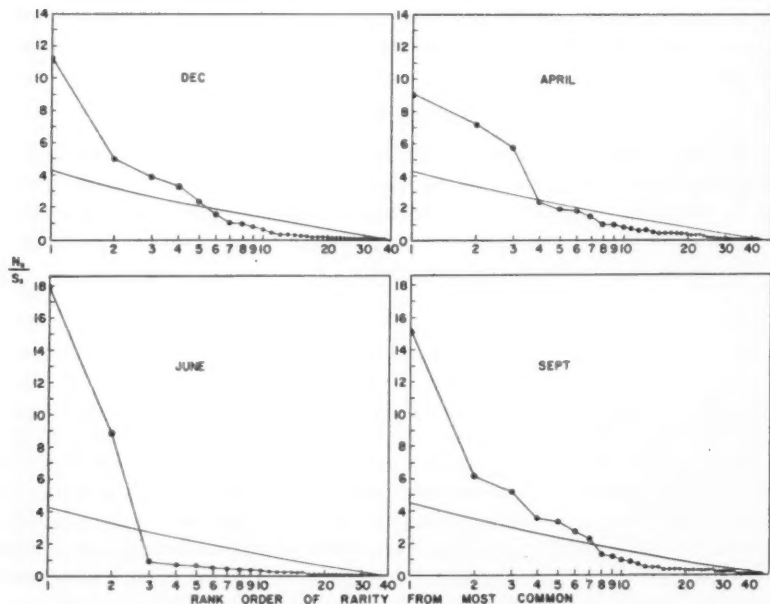
FIGURE 1. Abundance of individual species plotted against rank order for the planktonic diatoms of Braendegård Sø, for the four seasons, from Foged's data, showing type IV distributions. The unmarked line gives the type I distribution for a like number of species and individuals. The unit of population for each species is the ratio of total number of individuals (N_S) to total number of species (S_S).

heterogeneous diversity. Existence of the type IV distribution does not necessarily imply non-equilibrium, but if we assume niches are separated out of the niche-hyperspace with any boundary as probable as any other, we may conclude that either non-equilibrium in time or unexpected diversity in space are likely to underlie this type of distribution.

APPLICATION TO THE PLANKTON

Before proceeding to inquire how far plankton associations are either never in equilibrium in time or approach heterogeneous diversity in space in a rather subtle way, it is desirable to inquire how far ordinary homogeneous niche diversification may be involved. The presence of a light gradient in all epigean waters by day does imply a certain diversification, but in the epilimnia of lakes the chances of any organism remaining permanently in a particular narrow range of intensities is small in turbulent water. By day the stability of the epilimnion may well never be zero, but since what has to be explained is the presence of many species of competitors in a small volume of water, the role of small vertical variations is probably insignificant. A few organisms may be favored by peculiar chemical conditions at the surface film, but again this hardly seems an adequate ex-

planation. The Langmuir spirals in the wind drift might also separate motile
from non-motile forms or organisms of different densities to some extent but
again the effect is likely to be small and transitory. It is hard to believe
that in turbulent open water many physical opportunities for niche diversifi-
cation exist.

SYMBIOSIS AND COMMENSALISM

The mathematical theory of competition permits the treatment of commen-
sal and symbiotic relations by a simple change in sign of one or both of the
competition functions. It can be shown (Gause and Witt, 1935) that under
some conditions commensal or symbiotic species can occupy the same
niche. There is a little evidence that occasionally water in which one alga
has been growing may be stimulatory to another species (Lefèvre, Jacob and
Nisbet, 1952; see also Hartman, 1960) though it is far more likely to be in-
hibitory. Since some phytoplankters require vitamins and others do not, a
more generally efficient species, requiring vitamins produced in excess by
an otherwise less efficient species not requiring such compounds, can pro-
duce a mixed equilibrium population. It is reasonably certain that this type
of situation occurs in the phytoplankton. It is interesting to note that many
vitamin-requiring algae are small and that the groups characteristically
needing them (Euglenophyta, Crytophyceae, Chrysophyceae, and Dinophy-
ceae) tend to be motile. The motility would give such organisms an advan-
tage in meeting rare nutrient molecules, inorganic or organic. This type of
advantage can be obtained by non-motile forms only by sinking in a turbu-
lent medium (Munk and Riley, 1952) which is much more dangerous than even
random swimming.

ROLE OF PREDATION

It can be shown theoretically, as Dr. Mac Arthur and I have developed in
conversation, that if one of two competing species is limited by a predator,
while the other is either not so limited or is fed on by a different predator,
co-existence of the two prey species may in some cases be possible. This
should permit some diversification of both prey and predator in a homo-
geneous habit.

RESULTS OF NON-EQUILIBRIUM CONDITIONS

The possibility of synergistic phenomena on the one hand and of specific
predation on the other would probably permit the development of a somewhat
diversified equilibrium plankton even in an environment that was essentially
boundaryless and isotropic. It may, however, be doubted that such phe-
nomena would ever permit assemblages of the order of magnitude of tens of
species to co-occur. At least in homogeneous water in the open ocean there
would seem to be no other alternative to a non-equilibrium, or as MacArthur
(1960) would term it, an opportunistic community.

The great difficulty inherent in the opportunistic hypothesis is that since,
if many species are present in a really variable environment which is con-

trolling their competition, chance extinction is likely to be an important aspect of the process.[2] That this is not an important aspect of the problem, at least in some cases, is shown by the continual presence of certain dominant species of planktonic diatoms as microfossils in sediments laid down under fairly uniform conditions over periods of centuries or millenia. This is, for instance, clear from Patrick's (1943) study of the diatoms of Linsley Pond, in which locality *Stephanodiscus astrea*, *Melosira ambigua* and certain species of Cyclotella must have co-occurred commonly for long périods of time. It is always possible to suppose that the persistent species were continually reintroduced from outside whenever they became extinct locally, but this does not seem a reasonable explanation of the observed regularity.

IS THE PHYTOPLANKTON A VALID CONCEPT?

In view of the paradoxical nature of the phytoplankton, perhaps it is justifiable to inquire to what extent the concept itself has validity. In the ocean it is reasonably certain that the community is a self-perpetuating one, but in lakes it has long been regarded as largely an evolutionary derivative of the littoral benthos (for example, Wesenberg-Lund, 1908, pp. 323–325) and in recent years much evidence has accumulated to suggest that the derivation in some cases is not an evolutionary process in the ordinary sense of the word, but a process occurring annually, some individuals of a benthic flora moving at times into plankton. The remarkable work of Lund (1954, 1955) on Melosira indicates that the planktonic species of this genus become benthic, though probably in a non-reproductive condition, when turbulence is inadequate to keep them afloat. Brook (1959) believes that some of the supposed planktonic varieties of littoral-benthic desmids are non-genetic modifications exhibited by populations annually derived from the littoral. If most of the phytoplankton consisted of species with well-defined, if somewhat restricted, benthic littoral niches, from which at times large cultures in the open water were developed but perhaps left no descendants, much of our paradox would disappear. In the sea we should still apparently have to rely on synergism, predation and opportunism or failure to achieve equilibrium, but in fresh waters we might get still more diversity from transitory invasions of species which in the benthos probably occupy a heterogeneously diverse biotope like the soil fauna studied by Hairston (1959).

[2]The chance of extinction is always finite even in the absence of competition, but for the kind of population under consideration the arguments adduced, for instance, by Cole (1960) appear to the writer to be unrealistic. In a lake of area 1 km^2 or 10^6 m^2, in a layer of water only one meter deep, any organism present at a concentration of one individual per litre, which would be almost undetectibly rare to the planktologist using ordinary methods, would have a population N_0 of 10^9 individuals. If the individuals divided and the two fission products had equal chances of death or reproduction, so that in the expected case the population remained stable, the probability of random extinction (Skellam, 1955) is given by $p_e = [t/(1 + t)]^{N_0}$ where t is measured in generations. For large values of N_0 and t we may approximate by $t = -N_0/\ln p_e$. In the lake in question p_e would reach a value of 0.01 in 2.2×10^8 generations which for most phytoplankters would be a period of over a million years. Less than half a dozen lakes are as old as this, and all these are vastly larger than the hypothetical lake of area 1 km^2.

The available data appear to indicate that in a given lake district there is no correlation between the area of a lake and the number of species comprising its phytoplankton. This is apparent from Järnefelt's (1956) monumental study of the lakes of Finland, and also from Ruttner's (1952) fifteen Indonesian lakes. In the latter case, the correlation coefficient of the logarithm of the numbers of phytoplankton species on the logarithm of the area (the appropriate quantities to use in such a case), is −0.019, obviously not significantly different from zero.

It is obvious that something is happening in such cases that is quite different from the phenomena of species distribution of terrestrial animals on small islands, so illuminatingly discussed by Dr. E. O. Wilson in another contribution to this symposium. At first sight the apparent independence indicated in the limnological data also may appear not to be in accord with the position taken in the present contribution. If, however, we may suppose that the influence of the littoral on the species composition decreases as the area of the lake increases, while the diversity of the littoral flora that might appear in the plankton increases as the length of the littoral, and so its chances of diversification, increases, then we might expect much less effect of area than would initially appear reasonable. The lack of an observed relationship is, therefore, not at all inconsistent with the point of view here developed.

CONCLUSION

Apart from providing a few thoughts on what is to me a fascinating, if somewhat specialized subject, my main purpose has been to show how a certain theory, namely, that of competitive exclusion, can be used to examine a situation where its main conclusions seem to be empirically false. Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of trying to find out what has happened to cause its empirical falsification. It is, of course, possible that some people with greater insight might have seen further into the problem of the plankton without the theory that I have with it, but for the moment I am content that its use has demonstrated possible ways of looking at the problem and, I hope, of presenting that problem to you.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch, 1954, The distribution and abundance of animals. XV. 782 pp. Univ. of Chicago Press, Chicago, Ill.

Brook, A. H., 1959, The status of desmids in the plankton and the determination of phytoplankton quotients. J. Ecol. 47: 429-445.

Cole, L. C., 1960, Competitive exclusion. Science 132: 348.

Crombie, A. C., 1947, Interspecific competition. J. Animal Ecol. 16: 44-73.

Feller, W., 1939, Die Grundlagen der Volterraschen Theorie des Kampfes von Dasein in Wahrscheirlichkeitstheoretischer Behandlung. Acta Biotheoret. 5: 11-40.

Foged, N., 1954, On the diatom flora of some Funen Lakes. Folia Limnol. Scand. 5: 1-75.

Gause, G. F., 1934, The struggle for existence. IX. 163 pp. Williams and Wilkins, Baltimore, Md.

———— 1935, Vérifications expérimentales de la théorie mathematique de la lutte pour la vie. Actual. scient. indust. 277: 1-62.

Gause, G. F., and A. A. Witt, 1935, Behavior of mixed populations and the problem of natural selections. Amer. Nat. 69: 596-609.

Grinnell, J., 1904, The origin and distribution of the chestnut-backed Chickadee. Auk 21: 364-382.

Hairston, N. G., 1959, Species abundance and community organization. Ecology 40: 404-416.

Hardin, G., 1960, The competitive exclusion principle. Science 131: 1292-1298.

Hartman, R. T., 1960, Algae and metabolites of natural waters. *In* The Pymatuning symposia in ecology: the ecology of algae. Pymatuning Laboratory of Field Biology, Univ. Pittsburgh Special Publ. No. 2: 38-55.

Hutchinson, G. E., 1941, Ecological aspects of succession in natural populations. Amer. Nat. 75: 406-418.

———— 1953, The concept of pattern in ecology. Proc. Acad. Nat. Sci. Phila. 105: 1-12.

———— 1957, Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

———— 1959, Il concetto moderno di nicchia ecologica. Mem. Ist. Ital. Idrobiol. 11: 9-22.

Järnefelt, H., 1956, Zur Limnologie einiger Gewässer Finnlands. XVI. Mit besonderer Berücksichtigung des Planktons. Ann. Zool. Soc. "Vancimo" 17(1): 1-201.

Kohn, A. J., 1959, The ecology of *Conus* in Hawaii. Ecol. Monogr. 29: 47-90.

———— 1960, Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. Ann. Mag. Nat. Hist. 13(2): 309-320.

Lack, D., 1954, The natural regulation of animal numbers. VIII. 343 pp. Clarendon Press, Oxford, England.

Lefèvre, M., H. Jakob and M. Nisbet, 1952, Auto- et heteroantagonisme chez les algues d'eau dounce. Ann. Stat. Centr. Hydrobiol. Appl. 4: 5-197.

Lund, J. W. G., 1954, The seasonal cycle of the plankton diatom, *Melosira italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. J. Ecol. 42: 151-179.

———— 1955, Further observations on the seasonal cycle of *Melosira italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. J. Ecol. 43: 90-102.

MacArthur, R. H., 1957, On the relative abundance of bird species. Proc. Natl. Acad. Sci. 45: 293-295.

———— 1960, On the relative abundance of species. Amer. Nat. 94: 25-36.

Munk, W. H., and G. A. Riley, 1952, Absorption of nutrients by aquatic plants. J. Mar. Research 11: 215-240.

Nicholson, A. J., 1933, The balance of animal populations. J. Animal Ecol. 2(suppl.): 132-178.

———— 1957, The self-adjustment of populations to change. Cold Spring Harbor Symp. Quant. Biol. 22: 153-173.

Patrick, R., 1943, The diatoms of Linsley Pond, Connecticut. Proc. Acad. Nat. Sci. Phila. 95: 53–110.

Provasoli, L., and I. J. Pintner, 1960, Artificial media for fresh-water algae: problems and suggestions. *In* The Pymatuning symposia in ecology: the ecology of algae. Pymatuning Laboratory of Field Biology, Univ. Pittsburgh Special Publ. No. 2: 84–96.

Rand, A. L., 1952, Secondary sexual characters and ecological competition. Fieldiana Zool. 34: 65–70.

Ruttner, F., 1952, Plankton studien der Deutschen Limnologischen Sunda-Expedition. Arch. Hydrobiol. Suppl. 21: 1–274.

Skellam, J. G., 1955, The mathematical approach to population dynamics. *In* The numbers of man and animals, ed. by J. G. Cragg and N. W. Pirie. Pp. 31–46. Oliver and Boyd (for the Institute of Biology), Edinburgh, Scotland.

Udvardy, M. F. D., 1959, Notes on the ecological concepts of habitat, biotope and niche. Ecology 40: 725–728.

Wesenberg-Lund, C., 1908, Plankton investigations of the Danish lakes. General part: the Baltic freshwater plankton, its origin and variation. 389 pp. Gyldendalske Boghandel, Copenhagen, Denmark.
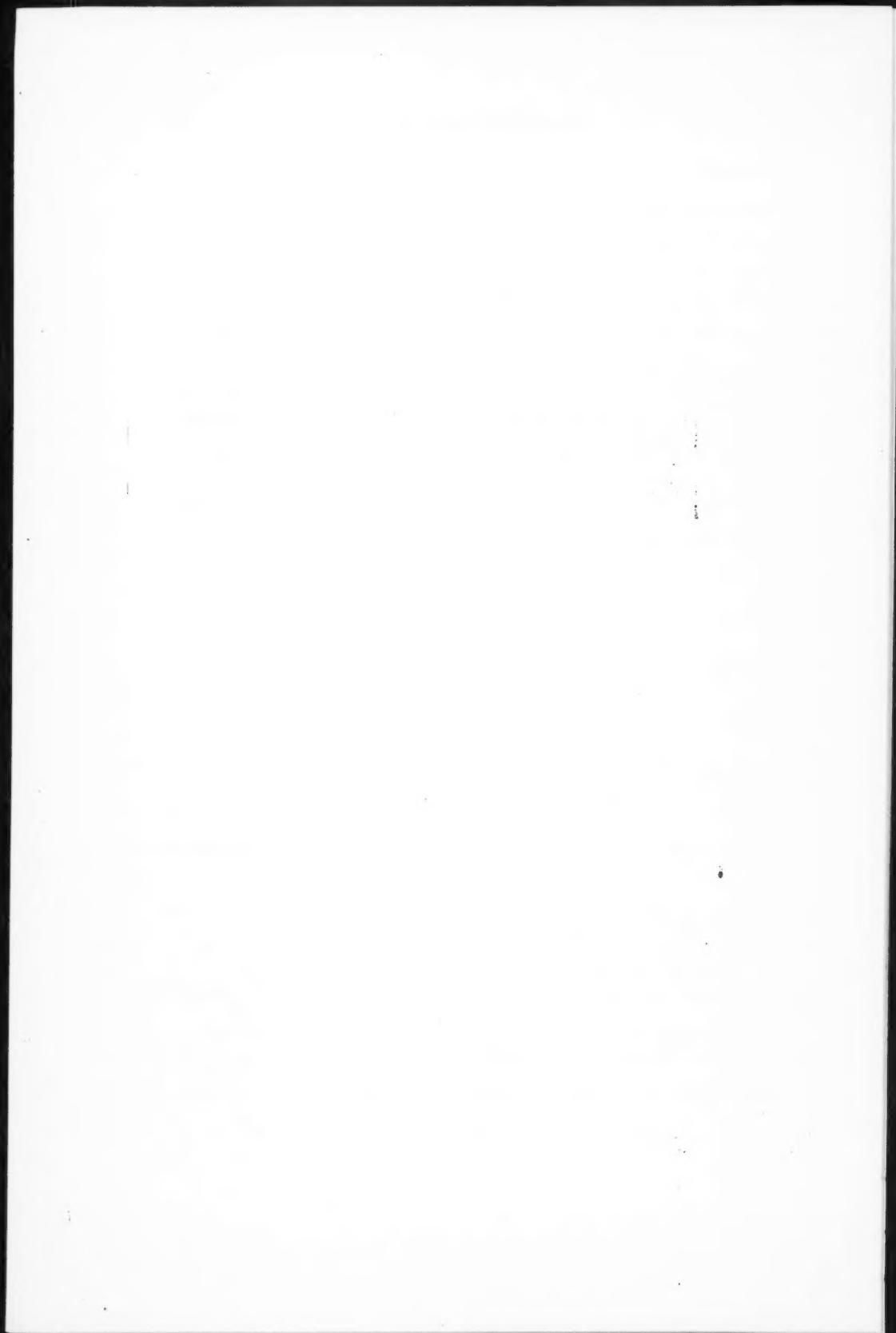
PRELIMINARY IDEAS FOR A PREDICTIVE
THEORY OF ECOLOGY*

L. B. SLOBODKIN

Department of Zoology, University of Michigan,
Ann Arbor, Michigan

We can all define ecology as the study of the interaction between organisms and their environment. Can we also state the goal of that study? This talk is essentially a presentation of my image of the goal of ecology with some discussion of the possible distance to that goal.

I hope that ecological research will eventually permit the production of a relatively simple program for a very large computer. This computer would be able to start with any desired set of descriptive information about an ecological community and from that information define the class of possible future evolutionary states that such a community might have.

It should be general enough to start with a geologist's picture of a preliving world and evolve life of some sort and from that evolve some recognizable ecological community. By a recognizable community I mean something as similar to any chosen terrestrial community as the forest of the Galapagos is to the Siberian Tundra or to the bottom of Block Island Sound.

It should be sufficiently precise so that given a description of pre-rabbit Australia, it would predict not only that rabbit introduction would be successful but that rabbit introduction in Australia would lead to decimation of English rabbits by a virus disease.

I am not able to construct such a program but I have some general ideas of how it might be constructed. In particular, I think I can describe the kinds of information that would be important in such a program. It might be noted that even if such a program proves uninteresting the attempt is of value since one measure of our comprehension of ecology is our ability to explain it in a clear unequivocal way to a student with absolutely no prior information about nature or science. An electronic computer is the only such student available.

Constructing the program will involve three processes. We must decide on the units to be used. We must also decide on the boundary conditions that define the class of realistic models of ecological communities. Finally, the operational procedures must be decided on. I will be concerned only with units and boundary conditions. The operational procedures will almost certainly be amplifications of the existing theories of population dynamics, population genetics and interspecific competition.

The numbers of individual organisms, their life expectancies, generation times, and reproductive rates, will certainly be of interest for each kind of organism in the program.

It must also be possible to translate the various kinds of animals into some common unit. This unit must be measurable and consistently relevant. For example, it cannot be either entropy, which is effectively unmeasurable in ecological situations, or a rare metal which may or may not be relevant in a particular community.

I would like to suggest that the appropriate unit to describe interactions between species is potential energy, measured as calories.

Hairston, Smith and Slobodkin (1960) state that energy universally limits ecological communities. They cite two facts:

1. Very little potential energy is stored as organic sediments, compared to the amount of potential energy fixed by photosynthesis during the same period.

This implies that energy is limiting to scavenger populations.

2. Green vegetation is only depleted by the herbivore populations when carnivores are absent or rare.

This implies that herbivores may not be food limited if carnivores are sufficiently abundant, but if the herbivores are not food (that is, energy) limited the carnivores must be.

Since the scavengers are energy limited and since, even if a particular population is not energy limited, the population preying on it is; all populations belong to energy limited communities.

The limitation of ecological communities by energy throughout evolutionary time is supported by direct calorimetry of whole animals. Slobodkin and Richman (ms.) have determined the calories per ash free gram of 16 species of animals from five phyla, using a micro-bomb calorimeter. Given a blindly chosen collection of species, a histogram of number of species versus caloric content might have been expected to have one of three mutually exclusive patterns. These are listed below:

1. A normal symmetrical distribution might have been anticipated from the fact that the biochemical potentialities of animals are so similar that there is only one mean caloric value for all species.

2. Different taxonomic groups might differ broadly in caloric content just as they do in morphology. This could be reconciled with the known biochemical similarities, since these are similarities in potentialities, which do not necessarily require all organisms to use their potentialities in the same way, nor to maintain a steady state store of biochemical components that would be identical from phylum to phylum.

3. A skewed distribution with a low modal value might arise from evolutionary considerations. Assume that energy has always been limiting. Also assume that there is always selective advantage to an individual that leaves a greater number of eventual progeny than the other members of the same

population.   These assumptions imply that any extra energy that becomes
available to an organism will usually be used for producing new organisms
rather than for increasing the caloric content per gram of the original indi-
vidual, since there is a clear selective advantage to increased reproduction
but no general advantage to high potential energy per gram.

The calorimetric data are presented in figure 1 and, while they are not
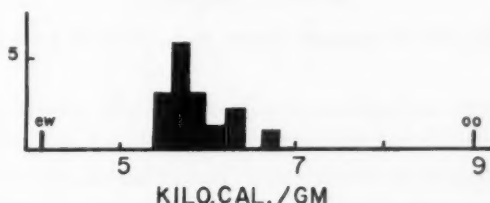conclusive, they conform to the assumption of universal limitation of com-
munities by energy.

FIGURE 1. Frequency distribution of calories per ash free gram of sixteen spe-
cies representing five phyla.   All data, except a determination for *Philenus leu-
copthalmus*, are taken from Slobodkin and Richman (ms.).   The Philenus determina-
tion was made by Richard Wiegert.

Why do a few species have relatively high caloric value?   Consider the
three highest values. One is a Tenebrio larva, about to pupate. The second
is a sample of Artemia nauplii, immediately after hatching and prior to the
development of a gut, and the third is a sample of *Dugesia tigrinum*, from a
rapidly growing laboratory population fed on Artemia nauplii.   All of the
other determinations were either of field populations or from laboratory pop-
ulations that were in a steady state.   The high values seem to be of two
types.   The first are organisms involved in a normal fast (that is, pupation
or embryonic development).   The animals must increase their caloric value
so as to carry with them what will be required for growth and maintenance.
The second are organisms that have available such a large food supply that
they cannot increase their size, activity, or reproductive rate sufficiently to
compensate for food intake.   Unless they lower their feeding rate they
get fat.

Extremes for biological material are indicated by the two short lines. The
higher value is that of olive oil (o o) and the lower, that for egg white (e w).

The tentative conclusion is that animals in general stay as lean as pos-
sible.   There is some minimum set of biochemical components required for
an animal's survival. If the energy supply available to an organism is in
excess of the maintenance requirements for this minimal set of components,
the additional energy will be used for reproduction or growth, but will usu-
ally not be stored in the organism as higher calories per gram. If the above
conclusions are valid, it should be found that forest herbivores in the spring
and summer, or perhaps even all year, have high caloric value per gram

while carnivores in general should be at the lower modal value. All animals from areas in which vegetation is denuded, in particular herbivores in the absence of carnivores, should be at the lower modal value. It may even prove possible to use direct bomb calorimetry to determine whether or not a species is food limited in nature.

I have so far indicated the likelihood that the appropriate units for the program will include potential energy as well as numbers of animals, age distributions, and genetic information.

BOUNDARY CONDITIONS

The following trivial example shows what is meant by a boundary condition:

"In the absence of migration, no population of any species can increase in numbers once it has decreased to a population size of zero."

A boundary condition is a statement that is empirically valid for all communities. Any program which will produce a community for which any boundary condition does not hold is an invalid program since it has produced an impossible community.

We can suggest a few non-trivial boundary conditions for the program. All of these must be further tested in the field.

One, suggested by G. E. Hutchinson in a presidential address to this society (Hutchinson, 1959), may be stated as follows:

"The ratio of mean size of food particle of any food-limited species that eats whole food organisms is to the mean size of food particle of the most strongly competing species as 1.25 is to 1."

The computer, to conform with this restriction must either guarantee the local extinction of one member of any species pair that simultaneously meets the requirements of being the most intensely competing pair that could be chosen from the community and of having a mean ratio of food particle less than 1.25 to 1, or it must permit one species of the pair to evolve towards a different food particle size.

The fact that species-abundance distribution curves conform to either MacArthur's distribution or to Hairston's modification of that distribution, as discussed by Hutchinson in this symposium, may also serve as a limit on the development of stable communities. (See Hutchinson, 1961.)

These and other generalizations may turn out to be consequences of more fundamental boundary conditions which cannot yet be stated explicitly.

There are two tentative boundary conditions that are largely based on experimental studies of Daphnia and Hydra populations in my laboratory. The Daphnia data have already been summarized (Slobodkin, 1960).

For any species we can define the quotient of the energy consumed per unit time by a predator on that species divided by the potential energy in the food available to the species itself as "food chain efficiency." The more reliable field estimates of this value, using entire trophic levels rather

than single species, range from c. 5 to c. 17 per cent. Laboratory estimates for *Daphnia pulex* populations have a maximum value of c. 8.5 per cent. *Hydra oligactis* populations in the laboratory have a maximum of approximately 7 per cent (figure 2). If a correction is made for the food actually consumed by the Daphnia, the maximum is c. 13 per cent. The Hydra value would also be increased if appropriate corrections were made.
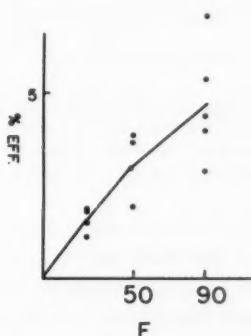

FIGURE 2. The food chain efficiency of sixteen *Hydra oligactis* populations as a function of predation rate, F (as defined by Slobodkin, 1960). The populations were maintained at four feeding levels on newly hatched Artemia in a culture solution suggested by W. F. Loomis (personal communication).

Since laboratory estimates, which are relatively free of sampling errors for the first two unrelated species analyzed experimentally, agree with each other and with field estimates, I would like to claim that much of the apparent diversity between field estimates is due to sampling error. If this is valid, a boundary condition might be stated in weak form as follows:

"Food chain efficiency cannot exceed some maximum value and this maximum is less than 15 per cent."

The laboratory data also suggest a numerical boundary condition.

If F represents the fraction of newborn animals removed by a predator, and P_F represents the steady state size of a population under constant predation rate F, then, for Daphnia populations, the following equation is valid:

$$\frac{P_F}{P_o} = 1 - \frac{F}{2 - F} \,.$$

The Hydra populations have higher variance than the Daphnia, but there is some reason to believe that the same equation still holds (figure 3). The large variance may be due in part to the impossibility of getting proper data on deaths in the Hydra populations and also to the greater sensitivity of Hydra populations to slight differences in culture medium.
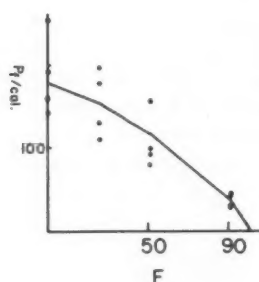
FIGURE 3. *Hydra oligactis* population size per unit food as a function of F. The line is derived by using P_F and F for each of the sixteen populations to calculate a theoretical value of P_o. The mean of these values was taken as the ordinal intercept and the theoretical values of P_F were computed from F and P_o.

The equation is free of fitted constants and can be derived from first principles (Slobodkin, 1959). It fits fairly well for two utterly unrelated species in the laboratory and there is some possibility that it may also adequately fit data from a North Sea fish population (see Gulland, 1961).

CONCLUSIONS

Similarities in caloric content over five phyla, field data on food particle size and species abundance distributions, laboratory and field studies of efficiency and the interaction between predation rates and population size, all suggest the possibility of constructing a general ecological theory which will permit an automatic computer to simulate, in a general sense, the kinds of landscapes we know.

How many boundary conditions are needed before a computer can simulate an evolutionary or ecological process is not now clear. We may already have enough.

The boundary conditions required are independent of taxonomy, time and place. They are derivable from laboratory and field data, occasionally supported by theoretical considerations and are immediately testable in the field.

This talk is at the beginning of a research program, not its culmination. In order to construct the kind of program I have outlined, the efforts of field, laboratory and theoretical workers will be required.

The laboratory ecological experiment has the advantage over field study of being repeatable, quick and cheap. It has an advantage over purely theoretical study in that experimental animals occasionally do things that no theoretician would have anticipated. The corresponding disadvantage is that the conclusions of the laboratory worker, while valid for his own restricted segment of nature, need not apply when the control conditions are released.

In one sense, the distinction between theoretician, laboratory worker and field worker is that the theoretician deals with all conceivable worlds while

the laboratory worker deals with all possible worlds and the field worker is confined to the real world. The laboratory ecologist must ask the theoretician if his possible world is an interesting one and must ask the field worker if it is at all related to the real one.

The laboratory experiment functions as an analogue computer to permit the development of certain generalizations. After field testing, these generalizations may be used as boundary conditions in a much more ambitious theoretical program than has hitherto been attempted.

LITERATURE CITED

Hairston, N., F. E. Smith and L. B. Slobodkin, 1960, Community structure, population control and competition. Amer. Nat. 94: 421–425.

Hutchinson, G. E., 1959, Homage to Santa Rosalia or why there are so many kinds of animals. Amer. Nat. 93: 145–159.

     1961, The paradox of the plankton. Amer. Nat. 95: 137–146.

Gulland, J. A., 1961, Comment on paper by Slobodkin. *In* Exploitation of natural populations, the second symposium of the British Ecological Society, ed. by E. D. LeCren and M. W. Holdgate. (In press) Blackwell's, Oxford, England.

Slobodkin, L. B., 1959, Energetics in *Daphnia pulex* populations. Ecology 40: 232–243.

     1960, Ecological energy relationships at the population level. Amer. Nat. 94: 213–236.

Slobodkin, L. B., and S. Richman, 1961, The caloric content per ash free gram of seventeen species of animals. (Ms.)

EXPERIMENTAL SYMPATRIC POPULATIONS OF CLARKIA*†

HARLAN LEWIS

University of California, Los Angeles, California

Sympatric wild populations serve as natural experiments from which critical information can be obtained concerning their capacity to maintain their genetic integrity. Such information is of paramount importance in drawing taxonomic conclusions, and much of the skill of taxonomy comes in evaluating allopatric populations in terms of what would happen if they were sympatric. The genetic interaction of sympatric populations is also of evolutionary importance because it may serve as a stimulus to evolution by creating new genetic combinations (Anderson and Stebbins, 1954) or it may result in the strengthening of existing barriers to gene exchange (Dobzhansky, 1940).

This paper describes the consequences of both natural and artificial sympatric association of two closely related species of flowering plants, *Clarkia biloba* and *C. lingulata* (Onagraceae). The experimental approach has been simple: a mixture of seeds of the two species has been sown at several sites in undisturbed habitats outside their natural area of distribution, and the resulting artificial populations have been studied in subsequent years. At the same time a natural experiment has been provided by the confluence of adjacent wild populations of these two species.

The genetic and phylogenetic relationship of *Clarkia biloba* and *C. lingulata*, as well as their distribution, variation, and breeding habit, has been presented elsewhere (Lewis and Lewis, 1955; Lewis and Roberts, 1956). Both are annual plants which occur in colonies of varying size on open, usually steep, slopes in the Oak-Digger Pine woodland of central California. The flowers are showy and normally outcrossed by various bees. They are, however, self-compatible and selfing may occur from a pollinator visiting more than one flower on the same plant.

Pollen exchange is apparently limited almost entirely to plants in the same colony; transfer between colonies has been found to be a rare event, even when they are separated by only a few meters (Lewis, 1953a). The number of flowers varies tremendously from plant to plant within a colony, reflecting primarily the variation in the habitat, and from year to year at the same site as a consequence of the vagaries of the climate. Each flower ordinarily sets about 30 seeds which are released slowly as the capsule gradually splits during a period of weeks. The seeds are about 1 mm. long

and .5 mm. in diameter; they have no wings or special means of dispersal and have a density slightly greater than water. Consequently, they usually fall within a few centimeters of the parent plant. Once on the ground they may be carried farther by ants or other small animals. But dispersal over greater distances frequently results from the harvest of whole plants or capsules by rodents who may carry them many meters before gleaning the seeds. The seeds have no dormant period and will germinate rapidly and uniformly under cool moist conditions any time after they mature. Experiments with other species, for example, *C. deflexa* (Lewis, unpubl.) and *C. dudleyana* (Snow, unpubl.), have shown that nearly all of the seeds of a given population germinate each year and consequently very few seeds are normally stored in the ground from one year to the next.

Clarkia biloba has an area of distribution in the Sierra Nevada foothills extending from Butte County in the north to the Merced River, west of Yosemite Valley, in the south, with a disjunct population near San Francisco Bay (figure 1). Within this area, three modally distinct geographical races have been recognized as subspecies. Only the southernmost of these, *C. biloba australis*, which is limited to the Merced River drainage, is involved in the present experiment. Consequently, in this paper, subsequent reference to *C. biloba* refers to this subspecies. *Clarkia lingulata*, on the other hand, is known only from two large populations, separated by about two miles, in the Merced River Canyon, where it grows adjacent to colonies of *C. biloba* (figure 2). *Clarkia biloba* and *C. lingulata* differ in external morphology only in the conformation of the petals, which are conspicuously notched at the apex in *C. biloba*. Hybrids between them are essentially sterile and this sterility has been shown to be attributable to chromosomal differences. *Clarkia biloba* has a gametic number of eight chromosomes whereas *C. lingulata* has nine chromosomes. Meiosis in the hybrid between them indicates that the additional chromosome of *C. lingulata* is homologous to parts of two chromosomes of the *C. biloba* genome. In this respect *C. lingulata* is a tertiary tetrasomic of *C. biloba* and, consequently, must have been derived from that species. In addition, they differ chromosomally by a large translocation and at least two paracentric inversions.

The location and extent of the colonies of both species in the Merced River Canyon was mapped in 1952. No mixed colonies were found; however, the lower population of *C. lingulata* was separated from the colony of *C. biloba* nearest to it by only 100 meters. The sites in this canyon occupied by these two species appear on visual inspection to be ecologically very similar if not equivalent. This is not to say that adjacent sites are identical, but rather that the habitats occupied by the two colonies of *C. lingulata* appear to be as different as those between *C. lingulata* and any of the colonies of *C. biloba.*

The colonies vary in time of flowering in the wild. For example, the lower colony of *C. lingulata* regularly begins to flower about two weeks earlier than the upper colony. Similar differences are found among the colonies of *C. biloba* which completely overlap the flowering time of *C. lingulata.* How-
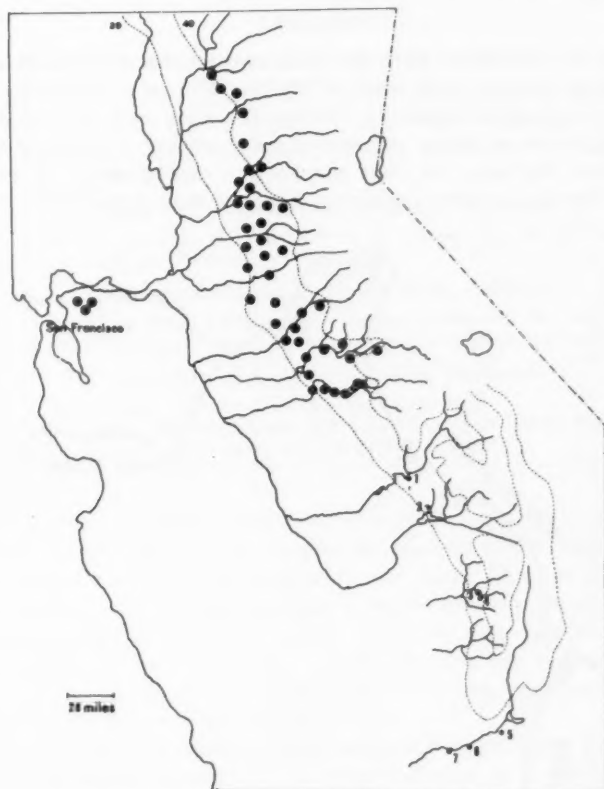
FIGURE 1. Outline of the central part of California showing the distribution of *Clarkia biloba* (●), *C. lingulata* (×), and location of experimental populations (numbered). See table 1 for localities. The 20 and 40 inch mean annual rainfall isohyetal lines (dotted) are based on a State of California Division of Water Resources map (1956).

ever, this is in a deep, steep-sided, sinuous canyon where exposure is constantly varying. In contrast to the variation observed in nature, progenies from wild seed grown in the garden under uniform cultivation showed no consistent differences in growth rate or flowering response suggestive of an adaptive difference either between colonies or between species. Progenies from the lower colony of *C. lingulata* and the adjacent population of *C. biloba* were also grown under 17 conditions of temperature and light in the Earhart Laboratories at the California Institute of Technology. The responses of the two progenies were parallel in every instance. This does not exclude the possibility, however, that the two species are differentially adapted to water stress, which was not a factor in that experiment.

Sites for the experiment were chosen in canyons that run roughly parallel
to that of the Merced River south of the natural area of distribution of *C.
biloba* and *C. lingulata* (figure 1). The specific sites (table 1) were selected
to have an exposure, slope, and associated vegetation comparable to those
of the native habitats. At least one species of Clarkia is indigenous to
each site because previous experience in establishing populations of Clarkia
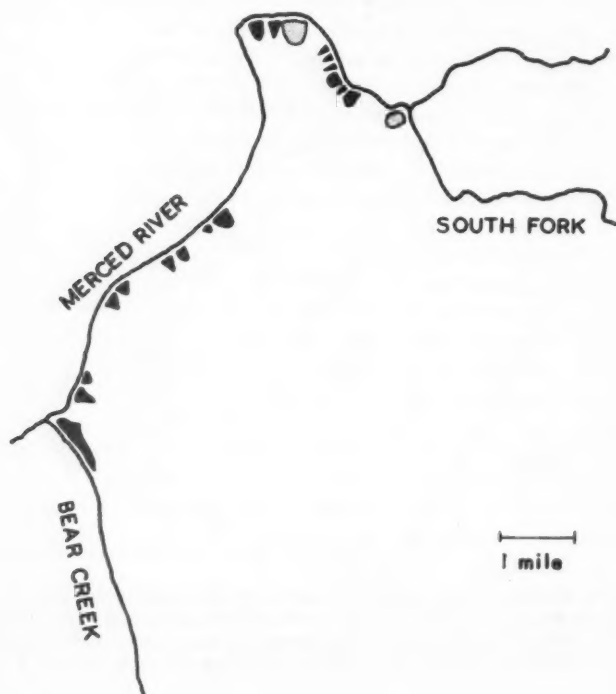
FIGURE 2. Extent and distribution of colonies of *C. biloba* (solid areas) and *C.
lingulata* (stippled areas) in the Merced River Canyon. The distribution of *C. biloba*
extends beyond the map west of Bear Creek.

in natural habitats (Lewis, unpubl.) has indicated this to be a necessary
condition for persistence of populations even for a few years. The most
conspicuous difference among the selected sites is in the amount of precipi-
tation and the frequency of effective storms. As shown in figure 1, the natu-
ral distribution of *C. biloba* and *C. lingulata* lies within an area character-
ized by an annual precipitation of 20 to 40 inches, except for the northern-
most localities of *C. biloba.* With respect to average rainfall, the four
northern experimental sites (1–4) are within the norm for the two species,

TABLE 1

Localities of experimental mixed populations of *Clarkia biloba* and *C. lingulata*.
Sown November 29–30, 1954.

San Joaquin River Drainage, Fresno County, California

1. Road to Kerckhoff Powerhouse, 3.3 miles west of the road from Auberry to North Fork.

Kings River Drainage, Fresno County, California

2. North side of Pine Flat Reservoir, 0.3 miles west of the road to Watts Valley at Trimmer.

Kaweah River Drainage, Tulare County, California

3. Mineral King Road, 4.0 miles from the road to Sequoia National Park.
4. Mineral King Road, 6.3 miles from the road to Sequoia National Park.

Kern River Drainage, Kern County, California

5. 1.6 miles south of Bodfish on the road to Havilah.
6. Breckenridge Mountain Road, 0.3 miles from Kern River Highway.
7. 8.5 miles east of the mouth of Kern River Canyon.

whereas the three southern sites (5–7) have less. But even within areas of equivalent rainfall, there is a conspicuous gradient in the frequency of effective storms from north to south in the prevailing direction of the winter storms (table 2). In the more southern sites the first rain often comes later and the last rain earlier; furthermore, there are characteristically longer periods of drought between storms. These droughts may have a greater influence on the length of the growing season than the total precipitation or the dates of the first and last effective rains.

Wild seeds for the experiment were gathered from the lower population of *C. lingulata* and the population of *C. biloba* adjacent to it. Because only a limited amount of seed can be harvested conveniently in the wild, seeds

TABLE 2

Storm patterns in the Sierra Nevada foothills 1950–1951 and 1958–1959. The first is representative of the norm; the second an exceptionally dry season.

	1950–1951								1958–1959							
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Merced River (Mariposa)	x	x	xx	xxxxx	xx		x		xxx	xx			x	x		
San Joaquin River (North Fork)	x	x	xx	xx	xx	xx		x	xxx	xx					x	
Kaweah River (Three Rivers)	x	x	x	xx	x	xx		x					xx		x	
Kern River (Kernville)		x	x	x			x		No record							

x Indicates at least half an inch of precipitation from a given storm.
    Data are from the weather stations listed in parenthesis, which are the closest stations to the natural and experimental sites in the river drainages indicated.

already on hand were multiplied by open pollination in the garden where the plants grow large and may produce a thousand capsules per plant in contrast to an average of ten or so in their natural habitats. The two progenies were grown in adjacent plots in the garden, two rows of *C. lingulata* on one side and five rows of *C. biloba* on the other. Open pollinated seeds were harvested separately for each species, estimated as to number, and then mixed uniformly in the proportion of seeds available; approximately five *C. biloba* to two *C. lingulata.* The mixture was then divided into seven equal parts of about 300,000 seeds each. The experimental plantings were made by broadcasting in the sites selected without disturbing the soil or cover. The density of sowing (approximately 3000 per m^2) was roughly comparable to what would have been deposited had there been a vigorous population already on the site. The sowings were made in November, 1954, coincident with the first winter rains and have remained unmolested since. Observations were made the following spring and have been repeated each year. Because plants that are not in flower cannot be distinguished as to species, frequencies have been determined only for the plants in flower at a given time and not for the population as a whole. Hybrids are easily recognized not only by the intermediate shape of the petals but also by the shrunken stamens which contain essentially no pollen.

OBSERVATIONS

The first season of observation showed reasonably large populations in the four northern sites but small or negligible populations in the three Kern River sites (table 3). Considering the low rainfall of the Kern River Canyon it is not surprising that initial populations were small and that rapid extinction occurred. Not only did these populations die out rapidly, but the few plants that came up the second and even the third year probably came from the initial sowing. This is certainly true of the planting near Bodfish (5) because the only two plants that flowered the first season withered and dried without producing seed. Nevertheless, 28 small plants were found flowering the next year. Inasmuch as there was little or no reproduction involved in the Kern River plantings, they will not be considered further. For the remaining four sites, however, direct evidence from hybridization indicates that the populations the second and subsequent years were derived in large measure from seeds produced *in situ.* The initial frequency of hybrids was three to five per cent (table 3) which represents the frequency of hybridization in the garden where the two species were growing in adjacent plots. The frequency of hybrids rose four or five fold in each of the four northern populations the following year, which would be expected from extensive outcrossing in a mixed population. Another indication that reproduction rather than stored seed was primarily responsible for populations subsequent to the first year was found in the relative spacing of the two species. In the first year the spacing appeared entirely random but on subsequent years plants of the same species tended to be clustered, presumably as a consequence of localized deposition of seeds at the base of the parent

TABLE 3

Frequency of *Clarkia biloba*, *C. lingulata*, and hybrids, in experimental mixed populations

	C. biloba† (per cent)				C. lingulata† (per cent)				Hybrids‡ (per cent)				Number of plants scored				Estimated size of population						
Locality*	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	5	6	7
Year																							
1955	47	75	31	55	53	25	69	45	5	3	3	3	759	956	1294	986	1000	1200	1500	1500	2	100	90
1956	31	85	50	53	69	15	50	47	20	16	13	15	130	273	278	556	200	350	400	600	28	100	...
1957	0	87	69	79	100	13	31	21	...	15	8	10	5	92	70	266	5	150	100	350	0	10	4
1958	...	100	46	72	...	0	54	28	...	...	...	17	0	19	27	151	0	25	40	150	0	1	0
1959	0	100	...	100	100	0	...	0	...	...	...	...	2	10	1	15	2	12	1	20	0	0	0
1960	...	100	74	100	...	0	26	0	...	...	14	19	0	5§	62	27	0	5	80	150	0	0	0

* See table 1 for localities.
† Based on total for the season. Hybrids excluded.
‡ Based on total plants scored.
§ Three plants were hybrids with *C. cylindrica*.

plants. Despite the evident reproduction, even the four northern populations declined in size each year for several years and the one on the San Joaquin River (1) is probably extinct. Of the other three, the population on the Kings River (2) barely survives, especially when one considers that of five plants found in flower in 1960, four were sterile hybrids, including three hybrids with the indigenous *C. cylindrica.* On the other hand, the two populations on the Kaweah River (3 and 4) are not only still extant but had sufficient vigor to increase in numbers in 1960 over the very low frequency observed in 1959, a year of exceptionally low rainfall (table 2).
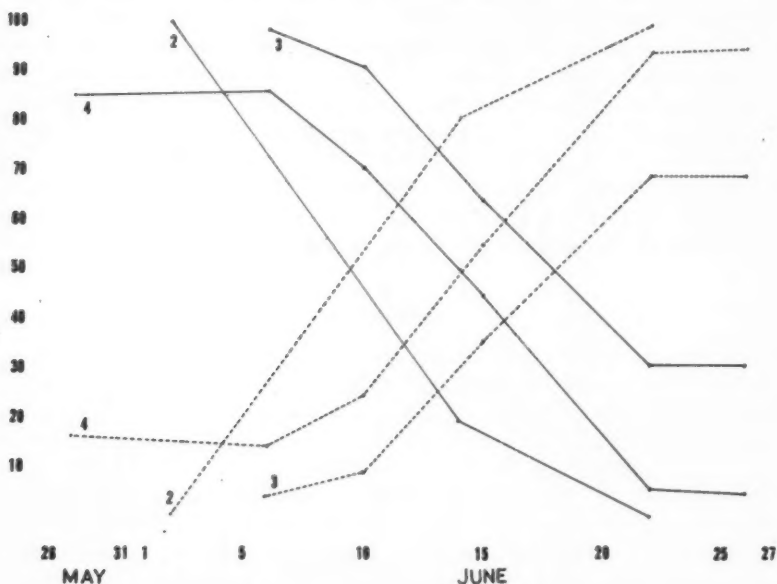
FIGURE 3. Frequency, in per cent, of flowering individuals of *Clarkia lingulata* (solid line) and *C. biloba* (broken line) in experimental populations 2, 3, and 4 on the dates indicated. See table 1 and figure 1 for localities. Observations for three years have been combined for each population. Hybrids have been disregarded.

The relative time of flowering of *C. biloba* and *C. lingulata* differed conspicuously and consistently in the experimental populations. Without exception, the earliest records of the season showed *C. lingulata* in great excess among the individuals in flower, whereas late in the season the great majority of the plants in flower were *C. biloba.* This pattern persisted from year to year. Repeated observations in any one year were not made sufficiently often to obtain a detailed measure of the shift in frequency between the two species. However, by combining the observations for the first three years, while population size was fairly large, a consistent picture emerges which is accurate with respect to the pattern of the change if not the detail (figure

3). These observations indicate quite clearly that not only is there a change in relative frequency of the two species as the season progresses but that they differ modally in time of flowering by about two weeks. Although the pattern was the same for each population, the dates of flowering differed from one site to another.

DISCUSSION

The establishment of experimental sympatric populations of *Clarkia biloba* and *C. lingulata* in natural habitats has permitted the two species to be compared directly under the same conditions of environmental stress. In some instances the experimental populations died out rapidly with little or no reproduction; in others, reproduction has been evident and the populations still persist after five generations. In those populations that have been most successful, *C. lingulata* has consistently matured earlier than *C. biloba* showing that the two species are physiologically different in at least this one respect. The question may still be asked, however, whether this difference is adaptive.

Early maturation would be expected to have a selective advantage and hence be adaptive under conditions in which the length of the growing season is limiting. It is not surprising, therefore, that differences in rate of maturation have repeatedly become established in the course of evolution. In Clarkia, for example, species which are morphologically and chromosomally most like the inferred ancestral stock of the genus have, at present, a center of distribution in northwestern California where the rainy season is long (Lewis, 1953 b). In the wild these species develop leisurely and bloom in the summer. In contrast, derivative diploid species, which today have a center of distribution in southern California where the rainy season is short, mature in the spring. When progenies of the two groups are grown in the garden in the absence of water stress, the difference in flowering time is evident but not so extreme as in the wild. Populations of one species may also show different rates of maturation in the garden correlated with the growing season in their natural habitats. For example, progenies of *C. unguiculata* from the drier lower limit of its distribution at the base of the Sierra Nevada (500 feet elevation) mature earlier than those from the upper limit (4000 feet elevation) at the same latitude (Lewis, 1953 a).

The length of the growing season, determined by available moisture, may be the most important factor limiting the southern distribution of *C. biloba*. The fact that *C. lingulata* is found at this southern limit may be a coincidence, but this seems very unlikely in view of the demonstrated differences in rate of maturation of the two species. In most years the growing season is doubtless long enough to permit normal maturation of both species, but unusually short seasons do occur in which *C. lingulata* would be expected to produce relatively more seeds than *C. biloba*. If they were growing together this would give an obvious advantage to the former, or, if they were growing in separate colonies one would expect *C. lingulata* to be less susceptible to extinction as a consequence of a series of unusually short growing seasons.

During the course of the experiment, the seasons have generally been dry, and an unusually dry season occurred in the winter of 1958–1959 at which time the experimental populations were reduced to very small numbers and the plants were generally depauperate. This might have been a season in which to compare the relative response of *C. biloba* and *C. lingulata* under severe water stress in a mixed population. Unfortunately, however, the experimental populations had already become drastically reduced in number and the response was too poor in all populations to provide a basis for comparison. Only one *C. lingulata* plant was observed in an experimental population and this plant was at a site (3) at which no *C. biloba* plants were observed. It seemed desirable, therefore, to reexamine the wild populations of *C. biloba* and *C. lingulata* in the Merced River Canyon to see what effect this exceptional year may have had on them. When these populations had been studied on several preceding occasions, no difference was noted in the vigor of the two species, that is, plants of both were of comparable size and produced comparable numbers of flowers and capsules. In 1959, however, some populations of *C. biloba* were not evident and the others consisted of notably depauperate plants. In contrast, the two populations of *C. lingulata* not only consisted of normal plants, but the area occupied by the populations was greater than that recorded in 1952. Furthermore, in this expansion *C. lingulata* had invaded the margin of an adjacent population of *C. biloba*. Our earlier studies showed that the lower colony of *C. lingulata* was separated by a linear distance of about 100 meters from the adjacent colony of *C. biloba*. The intervening area is a shallow ravine bordered by an oak thicket and is unsuitable for Clarkia. Nevertheless, within seven years *C. lingulata* has apparently been carried across this barrier, probably by rodents, and has become established as a small disjunct colony of about 200 individuals at the margin of a colony of *C. biloba* in territory that our earlier records indicate was occupied by *C. biloba*. The present zone of overlap is about three meters across, and as would be expected from the experimental populations, hybrids are frequent in and immediately adjacent to this narrow area of contact. Of particular interest for future investigation is the fact that we now have a natural experiment where the interaction of the two species can be followed in detail from year to year.

Our observations on wild populations can leave little doubt that *C. lingulata* in the last few years has been more successful than *C. biloba* in the Merced River Canyon. Furthermore, drought is the most obvious and the most likely climatic factor involved. The differential rate of maturity of *C. lingulata* and *C. biloba* in mixed populations would tend to substantiate this suggestion and offers an explanation for what has happened in the wild colonies. But *C. lingulata* has not been more successful than *C. biloba* in the experimental populations. In the two populations that still persist (3 and 4), *C. lingulata* is practically gone from one and in the other is apparently in no higher frequency than it was initially. Several factors contribute to an understanding of this apparent contradiction between behavior in the wild and in the experimental populations: (1) the initial frequency in the experi-

mental populations favored *C. biloba*, five to two; (2) the initial spacing of plants in the experimental population was random; (3) pollinators make no distinction between the species; (4) there are no apparent barriers to crossing; (5) the hybrids are essentially sterile.

Because the initial populations contained more than twice as many *C. biloba* plants as *C. lingulata* and because they were distributed in the population at random, *C. lingulata* had a greater chance of receiving pollen from *C. biloba* than from another *C. lingulata*, except at the beginning of the flowering period when few if any *C. biloba* were in bloom. But we have noticed that the earliest flowers to bloom in any population frequently do not set seed, presumably because the colony is not regularly visited by pollinators until a minimum number of flowers have opened. This would apply to the first *C. lingulata* flowers in a mixed population. By the time the first flowers of *C. biloba* open, however, pollinators are already being attracted by *C. lingulata* and interspecific hybridization would be encouraged. Inasmuch as the hybrids are essentially sterile, gametes of both species are lost to the population to the extent that hybrids are formed. But the loss by *C. biloba* would be proportionately far less because of the much greater opportunity for conspecific mating during most of the flowering period. The outcome of the experimental populations might have been very different had the two species been sown separately in adjacent plots at the same site rather than as a randomized mixture. The former would more closely approximate the situation in the natural experiment where the two species have now come into contact. Relative spacing has also undoubtedly been an important factor in the origin of *C. lingulata*.

Clarkia lingulata, as we have indicated, is unquestionably derived from *C. biloba* (Lewis and Roberts, 1956) and, as we have seen, has been able to migrate into the territory of *C. biloba* and locally replace it. In view of the results from the experimental populations, which indicate that *C. lingulata* is readily hybridized out of existence even when it comprises more than 25 per cent of the initial population, the question arises as to the conditions under which *C. lingulata* evolved from *C. biloba* and the circumstances that permit it to invade and displace the parental species.

The chromosomal differences that distinguish *C. lingulata* from *C. biloba* were probably introduced into a population of *C. biloba* more or less simultaneously as a consequence of a mutator genotype or possibly by hybridization with a related species such as *C. modesta* (Lewis and Raven, 1958). Two of the chromosomal differences, the added chromosome and the translocation, individually greatly reduce fertility in heterozygotes. Consequently, the transition to homozygosity must have been fairly rapid in terms of generations. But the double homozygote (that is, *C. lingulata*), although completely fertile and self-compatible, would be extremely susceptible to elimination in a population comprised primarily of individuals homozygous for the original *C. biloba* complement or any derivative chromosome arrangement that would produce hybrids of low fertility. Consequently, for the unique combination of chromosomes of *C. lingulata* to become characteristic

of a population, the initial plant (or plants) must have been isolated in some manner from *C. biloba.* Inasmuch as barriers to hybridization are not present, the initial isolation must have been spatial. This may have come about in either of two ways: (1) the original *C. lingulata* might have been transported by chance to a suitable site unoccupied by *C. biloba*, or, (2) all or most of the other plants in the population in which it originated may have died without issue. The first would seem to compound two improbable events, a suitable adjacent site unoccupied by *C. biloba* and chance transport of a seed of a particular genotype; the second requires a local catastrophe. Although improbable events undoubtedly play an important role in evolution, neither of the suggestions might seem reasonable were it not that we have seen wild colonies of Clarkia expand and contract or even disappear in course of a few seasons. We have, for example, made observations for a period of 14 years on adjacent colonies of *C. xantiana* that differ in flower color. During this time we have seen one large colony with pink flowers disappear while an adjacent colony with white flowers has not only persisted but has migrated into and now flourishes in the area previously occupied by the pink colony.

These observations on *C. xantiana* populations suggest that a suitable unoccupied adjacent site might have been available to a newly formed *C. lingulata* or that it might have survived a catastrophe that eliminated the remainder of the population in which it was formed. In addition, these observations on *C. xantiana* also suggest how *C. lingulata* has probably been able to invade the territory of *C. biloba*. In the Merced River Canyon, *C. biloba* is at one of the ecological limits of its distribution. Consequently, individual colonies are not stable and undoubtedly expand, contract, and occasionally become extinct, just as in the case of *C. xantiana.* The most likely explanation for the establishment of a disjunct colony of *C. lingulata* at the margin of an adjacent colony of *C. biloba*, therefore, is that the latter became temporarily contracted as a result of failure of plants at the margin to reproduce for a year or more. Before it was able to expand again, *C. lingulata* seeds were transported to the temporarily unoccupied area and a new colony became established. As both species have subsequently multiplied they have come into contact and are hybridizing.

Both species at present have more or less equal numbers of plants in the zone of contact. Consequently, they appear to be equally at a disadvantage from loss of reproductive capacity from hybridization, but at the same time they are able to perpetuate themselves by conspecific mating outside of the area of contact. An equilibrium may, therefore, be maintained except in years when a differential response would give an advantage to *C. lingulata*, or vice versa. However, if the general trend in the weather in California continues, there is no question in my mind as to which of the species will expand its range at the expense of the other. But whether *C. lingulata* and *C. biloba* continue to show mutual exclusion in the sites they occupy depends on whether or not a barrier to crossing evolves. With the development of such a barrier one would expect them to occur in mixed colonies with

modally different ranges of distribution, as is true of other closely related pairs of Clarkia species, for example, *C. unguiculata* and *C. exilis* (Vasek, 1958), with broadly overlapping ranges of tolerance.

SUMMARY

Clarkia lingulata is a tetrasomic derivative of *C. biloba.* It occurs locally at the southern limit of distribution of the parental species. They cross readily but the hybrids are essentially sterile. When first studied, they were found to occur in adjacent but not in mixed colonies. Since then, *C. lingulata* has extended its range and has become established at the margin of an adjacent colony of *C. biloba.*

Experimental sympatric populations were established by sowing a mixture of the two species in selected sites south of their natural area of distribution. Populations in the driest sites died out rapidly and showed little or no reproduction; in other sites reproduction has been evident and the populations still persist after five generations. In these artificial populations, *C. lingulata* has consistently matured about two weeks earlier than *C. biloba.* This suggests that *C. lingulata* is adapted to a shorter growing season than *C. biloba*, and may explain the occurrence of *C. lingulata* at the margin of distribution of *C. biloba* where the length of the growing season, determined by available water, is probably a limiting factor.

Observation of natural populations indicates that *C. lingulata* has been better adapted than *C. biloba* during recent years of low rainfall. Nevertheless, *C. lingulata* has not been more successful in the experimental populations. This is explained by: (1) the initial frequency which greatly favored *C. biloba*, (2) random spacing, (3) indiscriminate pollination, and (4) sterility of the hybrids. The conclusion is that *C. lingulata* has been hybridized out of the populations because it lost a much higher proportion of gametes in the formation of sterile hybrids.

The elimination of *C. lingulata* from mixed populations indicates that it must have been spatially isolated from *C. biloba* when it became established and, furthermore, that it should not be successful as a sporadic migrant into a population of *C. biloba.* The fact that it has successfully established itself at the margin of a colony of *C. biloba* can be explained by the expansion and contraction of colonies that occurs at the ecological limit of distribution. On this hypothesis, *C. lingulata* did not migrate into a population of *C. biloba* but became established in a temporarily unoccupied marginal site.

Although *C. lingulata* and *C. biloba* have broadly overlapping tolerances, they will not be able to grow in mixed colonies, except temporarily, unless a stronger barrier to hybridization develops.

LITERATURE CITED

Anderson, E., and G. L. Stebbins, 1954, Hybridization as an evolutionary stimulus. Evolution 8: 378–388.

Dobzhansky, Th., 1940, Speciation as a stage in evolutionary divergence. Amer. Nat. 74: 312–321.

Lewis, H., 1953a, The mechanism of evolution in the genus *Clarkia.* Evolution 7: 1–20.

　1953b, Chromosome phylogeny and habitat preference of *Clarkia.* Evolution 7: 102–109.

Lewis, H., and Margaret E. Lewis, 1955, The genus *Clarkia.* Univ. Calif. Publ. Botany 20: 241–392.

Lewis, H., and P. H. Raven, 1958, Rapid evolution in *Clarkia.* Evolution 12: 319–336.

Lewis, H., and Margaret R. Roberts, 1956, The origin of *Clarkia lingulata.* Evolution 10: 126–138.

Vasek, F. C., 1958, The relationship of *Clarkia exilis* to *Clarkia unguiculata.* Amer. J. Botany 45: 150–162.

THE NATURE OF THE TAXON CYCLE IN THE
MELANESIAN ANT FAUNA*

EDWARD O. WILSON

Biological Laboratories, Harvard University,
Cambridge, Massachusetts

The central contribution of biogeography to general biology is the description of the history of biotas. Aside from its relevance to evolutionary theory, biogeographic history has an immediate significance in population studies: we can expect that the role of individual taxa in ecosystems is influenced both by their geographic origin and by their duration as members of the community. Taxa penetrating from arid source areas will probably fill niches different from those filled by related taxa from moister regions. As a rule, newcomer taxa will undoubtedly affect communities differently from related taxa of long residence. Island biotas derived by radiation of limited stocks show important differences from those derived from more diverse "balanced" stocks, and so on. Of all the major factors that shape community organization, the variables of biogeographic history are probably the least understood. This is due simply to the great complexity of the subject and the tedious nature of its study, which requires revisionary taxonomy as the basic analytical instrument.

The purpose of this paper is to extend an earlier effort (Wilson, 1959a) to synthesize certain information on the zoogeography, speciation patterns and gross ecology of a limited fauna, the ants of Melanesia. In the first report just mentioned, only the subfamily Ponerinae was considered. Faunal sources and expansion patterns of the modern ponerine species were deduced; speciation was shown to be accomplished chiefly by multiple invasions accompanied by major shifts in habitat preferences. In this second study the following groups have been added, following more recent revisionary work by W. L. Brown (1958, 1960, and ms.) and the present author (1957, 1958a, 1959b, c, and ms.): Cerapachyinae, Dolichoderinae, and the myrmicine genera Pheidole, Crematogaster and Strumigenys. These include perhaps 50 per cent of all of the known Melanesian ant species. Not all of the taxa were well enough known to include in all of the analyses; hence, the particular taxa employed are cited with each analysis. Numerical data pertaining to the Asian fauna are based on the catalog by Chapman and Capco (1951), extended and corrected wherever possible by more recent revisionary work. Additional data have been taken from the valuable faunal monographs of Mann (1919, 1921). Emphasis has been shifted somewhat to

a consideration of certain aspects of the formation of individual faunas, the conditions underlying the origin of expanding taxa, and the interaction of expanding and confined taxa.

Certain expressions have special meanings in these analyses and must be defined at the outset:

"Central" tropical Asia: arbitrarily defined as mainland tropical Asia west to and including India and north to and including the "Oriental" portion of southern China, plus Sumatra, Borneo, and Java.

New Guinea: refers to the mainland only.

Expanding taxa: species extending natively over more than a single archipelago, or higher taxa containing such species. Far-ranging species extending beyond certain arbitrary limits are referred to as Stage-I species (see below).

Stage-I species, Asia-based: ranging from tropical Asia, the presumed source area, east to as far as the Moluccas or Micronesia, or beyond.

Stage-I species, New Guinea-based: ranging from mainland New Guinea, the presumed source area, to as far as the Moluccas, Solomon Islands, Micronesia, or any combination of these. Species ranging to Queensland, Aru, Manus, Bismarck Archipelago, or Waigeo but not beyond are arbitrarily not classified as Stage-I.

Stage II and III species: Species of more restricted ranges interpreted as belonging to other phases of the speciation cycle (see Wilson, 1959a).

RELATION OF AREA TO FAUNAL NUMBER

It can be shown that as the area of islands increase, resident faunas of some animal groups logarithmically increase approximately as

$$F = bA^k,$$

where F is the number of resident species and A is the land mass in square miles. In the Ponerinae-Cerapachyinae of Melanesia and the Moluccas, k is approximately 0.7 (figure 1). It is a fact of uncertain significance that k shows considerable variation among different major animal groups and among different faunas. In the Carabidae and herpetofauna of the Greater Antilles and associated smaller islands it is approximately 0.3. In the breeding land and fresh-water birds it is approximately 0.4 in the islands of the Sunda Shelf (Indonesia) but close to 0.5 in the islands of the Sahul Shelf (New Guinea and environs).

The considerable scatter in the area-fauna measurements of the Ponerinae-Cerapachyinae is evidently due to two principal factors: (1) differences in ecology; for example, Kandavu and Vanua Levu are so extensively cultivated as to support smaller indigenous faunas; (2) simply incomplete collecting, which undoubtedly accounts in large part for the seeming paucity of the Halmahera, Bismarcks, and Rennell faunas.

If only those islands are considered which are along the main line of the Sunda-Melanesian arc, which still possess large tracts of native vegetation,
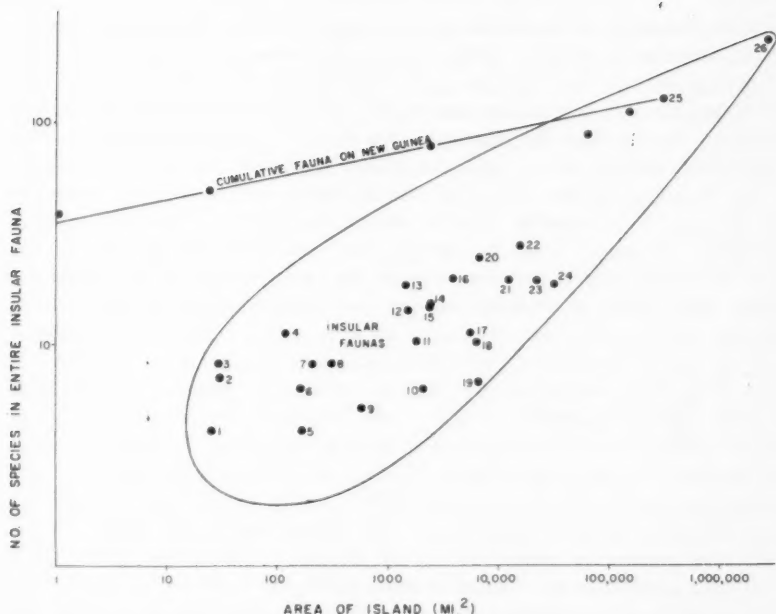
FIGURE 1. The relationship of area to number of ponerine and cerapachyine ant species in the faunas of various Moluccan and Melanesian islands. 1. Ternate; 2. Malapaïna; 3. Ugi; 4. Florida; 5. Kandavu; 6. Taviuni; 7. Ndeni; 8. Amboina; 9. Rennell; 10. Vanua Levu; 11. Espiritu Santo; 12. San Cristoval; 13. Santa Isabel; 14. Malaita; 15. Waigeo; 16. Viti Levu; 17. New Hebrides (entire); 18. Ceram; 19. Halmahera; 20. Fiji (entire); 21. New Britain; 22. Solomons (entire); 23. Bismarcks (entire); 24. Moluccas (entire); 25. New Guinea; 26. central tropical Asia. The cumulative New Guinea localities given in the upper curve are as follows: lower Busu River; triangle formed by the lower Busu River, Didiman Creek, and Bubia; all of the Huon Peninsula; northeast New Buinea; northeast New Guinea plus Papua; all of New Guinea.

and which have been reasonably well collected, a much stronger correlation appears, with a slope (k) of about 0.6 and an origin (b) of between two and three. If literally true, this would mean that an island one square mile in area can hold only two or three species, while one under one-tenth of a square mile could hold only one species. These predictions fit very closely the actual faunal size of very small islands in Polynesia, which has been better analyzed (Wilson and Taylor, ms.).

From the details of this analysis, an interesting fact emerges: the size of individual faunas is not correlated with their nearness to the source areas of tropical Asia and New Guinea. Intuitively, one might expect the Moluccas, which are main stepping stones of faunal movement to and from New Guinea, to have a larger fauna than the more remote, peripheral Solomons and Fiji. Yet the reverse is true. The best collected Moluccan Islands (Ternate,

Amboina, Ceram) have somewhat sparser faunas than the best collected parts
of the Solomons and Fijis.   It is true, on the other hand, that the number
of phylogenetic stocks (that is, species groups) declines significantly from
the Moluccas and New Guinea eastward.   But the total number of species
does not deviate from the expected.   On Fiji a relatively small number of
stocks have diversified to "fill" the Fijian "quota."

   The data suggest that individual insular faunas approach upper limits set
by the size of the islands.   In other words, they are in a saturated or near-
saturated condition.   It can be inferred that, as a rule, new species can in-
vade an island only if resident species are extinguished to make room for
them.   Other lines of evidence support this generalization.   In New Guinea
lowland rain forests, common native ant species show patchy distributions
that are poorly correlated with habitat and which result in a limitation of
size of local faunas (Wilson, 1958b).   In coconut plantations of the Solomon
Islands, mixed populations of native and introduced species show clear-cut
mosaic distributions determined less by vegetation than by interaction and
replacement of competing species (E. S. Brown, 1959).   The process of re-
placement usually involves intercolonial fighting, and it strictly limits the
size of faunas of small sample areas.   The phenomenon is not unique.   Segre-
gation of species by competition in the British ant fauna has already been
well demonstrated in the studies of Brian (1952, 1955, 1956a, 1956b).

   It is reasonable to expect that the tendency toward mosaic distributions
will result in a pattern of fixation-versus-elimination of competing species
on very small islands.   In Polynesia, where data are now complete enough
to allow a reasonably full analysis (Wilson and Taylor, ms.), this proves to
be the case.   The mosaic pattern is extended to include entire islands and
even archipelagoes.   On the major islands of Melanesia and Polynesia, and
on islands as small as Nuku Hiva and Hiva Oa, members of the same spe-
cies groups commonly exist together.   But among yet smaller islands, such
as Rotuma, Raratonga, and Fakaofo, related species tend to exclude one
another in an unpredictable manner, forming mosaic patterns.   On still
smaller islands, intergeneric replacement is evident.   The latter phenomenon
is consistent with the findings of Brown, who observed intergeneric strife
and replacement as a common occurrence in the coconut plantations of the
Solomons.   As a result of this phenomenon of small-faunal diversification,
the summed faunas of entire archipelagoes are larger than could be predicted
from knowledge of a limited sample of individual insular faunas.   As noted
already, a similar process operates at the level of local faunas of large is-
lands to enrich the total insular fauna.   The phenomenon can be conven-
iently referred to as *faunal drift*.   This expression is used simply to infer
that the composition of small local faunas varies in an unpredictable man-
ner, that is, there is a subjective element of randomness.   It remains to be
seen to what extent faunal drift is really the result of chance phenomena
such as accidents of colonization.

   We can next inquire whether faunal drift results in the stabilization of
local faunal size, with the result that local faunal size, that is, the number

of species occurring in a set sample area, is independent of island size and hence of the total number of species occurring on the island. It turns out that this is not the case. As shown in figure 2, local faunal size increases with the area of the island. Local fauna here is defined as the fauna of an area of approximately one square mile (2.5 km.^{2}) in the lowlands, and encompassing both rain forest and marginal habitats.
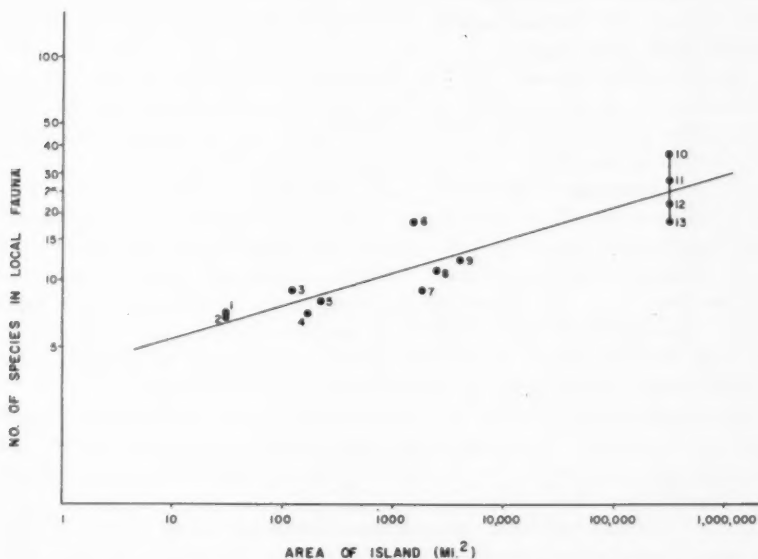
FIGURE 2. The relationship of the area of Melanesian islands to the number of ponerine and cerapachyine species occurring within local faunas on them. The following local faunas are given: 1. Pawa, Ugi; 2, Malapaina; 3. Tulagi, Florida; 4. Somo Somo, Taveuni; 5. Graciosa Bay, Santa Cruz; 6. Fulakora, Santa Isabel; 7. Luganville, Espiritu Santo; 8. Auki, Malaita; 9. Nadarivatu, Viti Levu; 10-12. localities on New Guinea.

With respect to total faunal size in Melanesian ants, the following generalization holds: when the total number of species occurring on an island does not exceed ten species, all of them can be expected to occur in the local fauna, as just defined. When the total fauna includes about 20 species, the local fauna contains from approximately half to all of them. When the total fauna contains over 100 species (New Guinea), local faunas contain only between ten and 30 per cent.

As the sample area on a great island such as New Guinea is progressively decreased, the decrease in local faunal size is less marked than that in decreasing sample areas comprising whole islands (figure 1). Thus the level of "saturation" is higher in local faunas of large islands than in small ones.

THE SOURCES OF THE EXPANDING SPECIES

Two geographical criteria have been used in this study to estimate the origin of a given expanding species: (a) primarily, the center of the present range of the species, and (b) secondarily, the site of maximum diversification and geographical center of the ranges of its closest relatives. In practice the two predicted centers nearly always coincide, at least to the nearest two adjacent archipelagoes. Following are examples of several of the most diverse distribution patterns that have been encountered and the decisions made about them.

(1) *Diacamma rugosum.* Ranges continuously from India to New Guinea. Two distantly related endemic species occur in the Moluccas but the great bulk of the genus occurs in the Oriental Region and is actively speciating and spreading from there. Estimated origin: Oriental Region.

(2) *Odontomachus tyrannicus.* Occurs over most of New Guinea and in the peripheral islands of New Britain, Japan, and Waigeo. The closest related species are limited to New Guinea. Estimated origin: New Guinea.

(3) *Odontomachus saevissimus.* Occurs continuously from the Moluccas to New Britain. A closely related species, *emeryi*, is endemic to the Solomons. Speciation of other members of the *saevissimus* group is active in both the Oriental Region and in New Guinea but primarily in the latter. Estimated origin: New Guinea.

(4) *Odontomachus simillimus.* Occurs continuously from Ceylon through most of Polynesia. The three most closely related species occur in New Guinea; one, *cephalotes*, has spread to offshore islands from New Guinea. Estimated origin: New Guinea.

(5) *Platythyrea parallela.* Ranges more or less continuously from Ceylon to Samoa and occurs (introduced by commerce) in the Society Islands. The bulk of the genus occurs in the Oriental Region. Only one other species, *quadridenta*, is native to Melanesia; this is very distinct from *parallela*, being related to the Oriental *sagei*. Estimated origin: Oriental; questionable.

(6) *Ponera biroi.* Widespread on New Guinea, occurs in addition on New Britain and in the Solomons. A closely related species, *eutrepta*, is limited to Fiji, but the other three members of the *biroi* species groups are endemic to New Guinea. Estimated origin: somewhere in New Guinea plus Bismarcks; New Guinea is the more likely specific source, but both archipelagoes should be included jointly in statistical measures of faunal origins.

The patterns of distributions of several ant subfamilies in Melanesia are summarized in figure 3. Here are presented the limits of distribution of species centered in Melanesia. Those judged to be penetrating from the Oriental Region are omitted. It will be noted that the centers of distribution of the great majority of these Melanesian species are in New Guinea or, at most, New Guinea plus the Bismarck Archipelago. From this center species can be observed in virtually every stage of expansion, some reaching only to immediately adjacent archipelagoes, others outward beyond the Moluccas and Fiji. The ranges tend to be equiformal, that is, extending in both direc-

WESTERN RANGE LIMIT

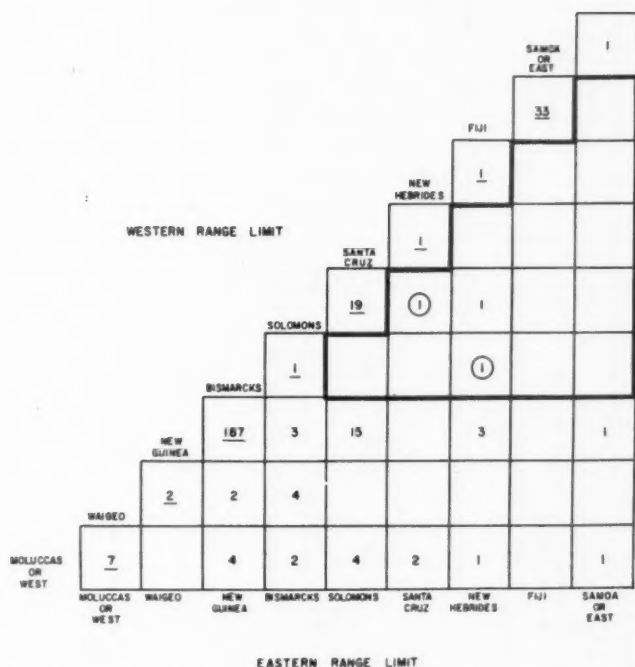| Western \ Eastern	MOLUCCAS OR WEST	WAIGEO	NEW GUINEA	BISMARCKS	SOLOMONS	SANTA CRUZ	NEW HEBRIDES	FIJI	SAMOA OR EAST
SAMOA OR EAST									1
FIJI								33	
NEW HEBRIDES							1		
SANTA CRUZ						1			
SOLOMONS					19	(1)	1		
BISMARCKS				1			(1)		
NEW GUINEA			167	3	15	3			1
WAIGEO		2	2	4					
MOLUCCAS OR WEST	7		4	2	4	2	1		1

EASTERN RANGE LIMIT

FIGURE 3. Range limits of Melanesian species of Ponerinae, Cerapachyinae, Dolichoderinae, Pheidole, Crematogaster, and Strumigenys. The number of endemic species on each archipelago is underscored.

tions from New Guinea, and in the sum their limits form concentric rings centered on New Guinea. The pattern in the vicinity of Fiji is notably different. Although 33 species are endemic to Fiji, not a single species extends from there to adjacent archipelagoes. There is, in striking contrast to New Guinea, no sign of the movement of species originating on Fiji outward from that archipelago. The Solomons fauna presents a similar pattern to that around Fiji; although being closer to the complex fauna of New Guinea, it is more difficult to analyze. Three species extend from the Solomons to immediately adjacent archipelagoes. Two, however, are evidently relicts: *Anochetus isolatus*, which is a member of a fragmented and evidently receding superspecies (Wilson, 1959b), and an undescribed species of Crematogaster (Orthocrema), which is known only from Espiritu Santo and New Ireland. The third species, *Turneria pacifica*, is classified as originating in the Solomons. The percentage of autochthonous expanding species is still much smaller in the Solomons than in New Guinea, or even New Guinea and the Bismarcks measured jointly.

In table 1 is presented an analysis of the differences in contributions of expanding species of New Guinea, the Solomons, and the Fiji. It will be

TABLE 1

The relation of land area to percentage of expanding species in the resident fauna

Taxa included	Opposed land masses	Number of endemic species	Number of autochthonous expanding species	Difference in frequencies of expanding species	χ^2	p	χ^2_c	Pc	Statistical interpretation of frequency difference
Ponerinae, Cerapachyinae, Dolichoderinae, Myrmicinae	New Guinea	187	35						
	Solomons	19	1	0.108	1.59	0.20	0.86	0.30	Not significant
Ponerinae, Cerapachyinae, Dolichoderinae, Myrmicinae	New Guinea	187	35						
	Fiji	33	0	0.158	5.86	0.02	4.61	0.03	Significant
Ponerinae, Cerapachyinae, Dolichoderinae, Myrmicinae	New Guinea plus Bismarcks	191	32						
	Fiji	33	0	0.143	5.25	0.02	4.02	0.04	Significant
All ant species	New Guinea plus Bismarcks	...	...						
	Fiji	58	1	(0.120)	6.25	0.01	5.79	0.02	Significant

The frequencies of expanding species originating from Melanesian archipelogoes of different areas are compared. The larger proportion of such species originating from New Guinea is significant at the 95 per cent confidence level with reference to Fiji but not with reference to the Solomons, because of the smaller sample of species from the latter islands. In the last two rows New Guinea and Bismarcks are combined to give the lowest possible estimate of autochthonous expanding species. In the last row the composition of the total Fijian ant fauna is given; that of the total New Guinea-Bismarcks fauna cannot be directly estimated and is assumed to be the same as in the better analyzed taxa, comprising approximately 50 per cent of the species. Both χ^2 and Yates' correction of χ^2 for assumed continuous distribution are given.

noted that whereas approximately 15 per cent of the New Guinea (or New
Guinea plus Bismarcks) fauna has expanded to adjacent archipelagoes, none
of the Fijian species have, and only one, or five per cent, of the Solomons
fauna can be considered to have done so. The difference between the New
Guinea and Fijian faunas is significant at the 95 per cent level. That be-
tween the New Guinea and Solomons faunas is not significant, but this could
be attributed simply to the smaller available sample.

TABLE 2

The relation of land area to percentage of contributed interpenetrating
species in the Ponerinae and Cerapachyinae

Competing faunas	Per cent share of land mass	Per cent share of native species	Per cent contri- bution of inter- penetrating Stage-I species	χ^2	χ^2_c	$\frac{P}{P_c}$	Statistical interpre- tation
Fiji vs. New Guinea	2.28	16.10	$\frac{0}{1}=0$	...	...	$\frac{...}{>0.50}$	Not signifi- cant
Fiji vs. central tropical Asia	0.25	9.44	$\frac{0}{2}=0$	...	...	$\frac{...}{>0.50}$	Not signifi- cant
Solomons vs. New Guinea	5.22	17.76	$\frac{0}{9}=0$	...	0.86	$\frac{...}{ca.\,0.30}$	Not signifi- cant
Solomons vs. central tropical Asia	0.57	10.50	$\frac{0}{10}=0$	...	0.60	$\frac{...}{ca.\,0.40}$	Not signifi- cant
New Guinea vs. central tropical Asia	10.93	35.21	$\frac{2(\times 100\%)}{18}=11.11$	4.40	3.40	$\frac{0.04}{0.06}$	Signifi- cant

The ponerine-cerapachyine faunas of opposing pairs of land masses are compared
with reference to the exchange between them of interpenetrating species. No sig-
nificant difference exists between the share of land mass and share of interpene-
trating species. The χ^2 and probability values apply to the difference between per-
centage share in combined native faunas and percentage share in combined inter-
penetrating species. In the case of New Guinea (versus central tropical Asia) the
difference is significant at the 95 per cent confidence level. Samples of species
from other Melanesian islands are too small to allow a formal test, but even so it
will be noted that the contribution of interpenetrating species by the smaller archi-
pelogoes is consistently nil. (See also figure 4.)

We may now turn to another index of faunal dispersal, the degree to which
species of one fauna penetrate other faunas. The *interpenetration* of com-
peting faunas is measured simply as the number of species extending from
one archipelago and colonizing another. Here it is possible to compute not
only the exchange of faunas within Melanesia but also that between Melane-
sia and tropical Asia. In table 2 are given the known amounts of interpene-

tration within the Ponerinae and Cerapachyinae of central tropical Asia, New
Guinea, the Solomons, and Fiji. These measures are coupled with land mass
and total faunal size and the correlations shown graphically in figure 4. It
will be seen that the percentage contribution of interpenetrating species of a
given archipelago is nearly the same as its percentage share of the land
mass. Note that it is theoretically possible, and interesting, to substitute
percentage share of population size for percentage share of land mass. The
contribution of interpenetrating species is not linearly correlated with per-
centage share of total faunal size, as one might intuitively expect. The dif-
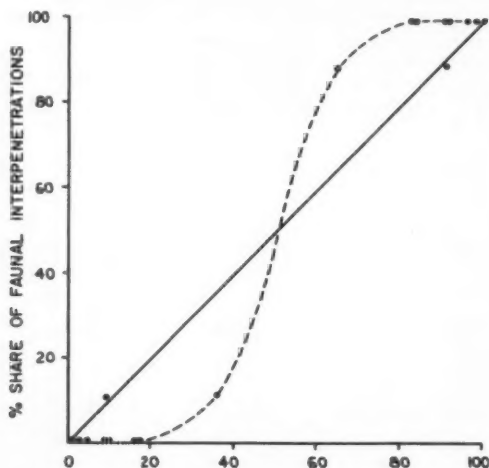

FIGURE 4. The correlation of share of interpenetrating ponerine and cera-
pachyine species with share of land area (solid circles and line) and with share of
total number of species in competing pairs of archipelagoes (open circles and
dashed line). See also table 2 and further explanation in the text.

ference between these two measures is significant at the 95 per cent level
in the case of New Guinea versus central tropical Asia. A formal statistical
difference cannot be demonstrated in the case of the smaller archipelagoes,
due to smallness of sample size. But the relationship is numerically abso-
lute in each case, that is, the contribution of interpenetrating species of the
smaller archipelagoes is zero.

Faunal interpenetration is here defined as a direct indicator of faunal
dominance. This interpretation is clarified if we consider what the joint con-
tributions would be to an intermediate island of exactly equal accessibility.
The faunas of the two source archipelagoes would "compete" to fill the is-
land's faunal quota. It can be inferred that their percentage share of faunal
contributions would be the same as the percentage share of interpenetrating
species exchanged between them.

BIOLOGICAL CHARACTERISTICS OF EXPANDING SPECIES

The Melanesian ant fauna appears to stem almost exclusively from species moving out of three source areas: tropical Asia, New Guinea, and Australia. In most of the analyses to follow, only the Ponerinae, Cerapachyinae, and selected myrmicine genera will be considered. All of the expanding species in these taxa are either Asia- or New Guinea-based, simplifying the procedures. It may be noted that Australia-based expanding species in the Dolichoderinae appear to conform to the general biological characterizations to be described in the other groups.
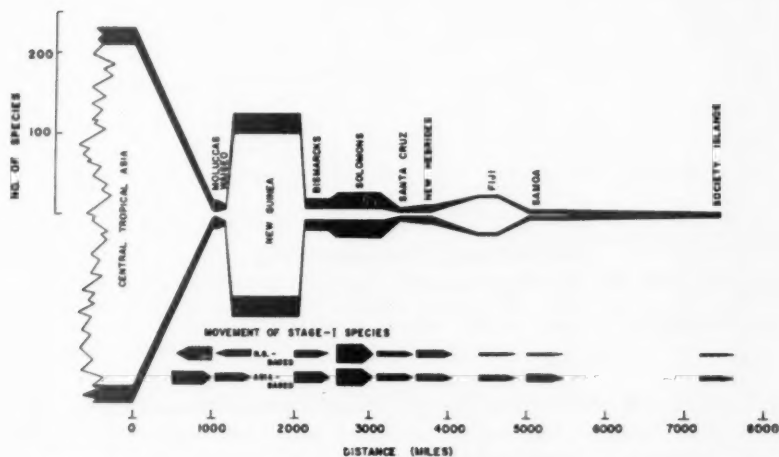

FIGURE 5. The partition of ponerine-cerapachyine species of various archipelagoes into Stage I (shaded) or Stage II and III (blank). The Stage-I species are further distinguished as Asia-based or New Guinea-based.

In figure 5 are given the partitions of some of the faunas of major Oriental-Pacific archipelagoes into speciation stages. A significant characteristic can be seen on inspection: the absolute number of Stage-I (expanding) species does not vary greatly from island to island. What varies markedly is the proportion of Stage II and III species (endemics or near-endemics). As the size of the island decreases, the absolute number of Stage-I species declines only slowly, while that of Stage II and III species declines rapidly. On islands the size of Waigeo and Ndeni (Santa Cruz) in the main Melanesian arc, Stage-I species predominate (figure 6). Fiji shows the same negative correlation between island size and proportion of Stage-I species, but the proportionality remains overall much lower.

As shown elsewhere (Wilson, 1959a) the expanding (Stage-I) species in New Guinea occur preponderantly in marginal habitats. Marginal habitats are defined as those containing the smallest number of ant species. They
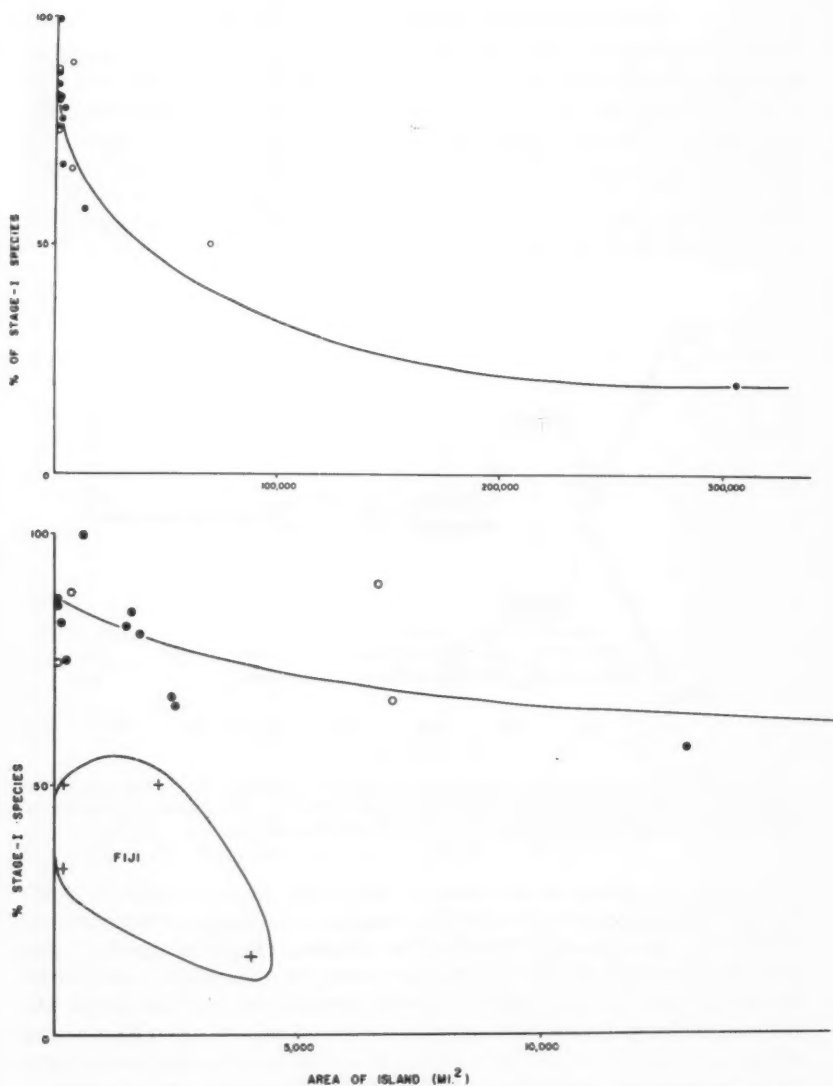
FIGURE 6. The percentage of Stage-I ponerine-cerapachyine species on islands with various areas. Open circles: Moluccas and Celebes. Closed circles: Melanesia exclusive of Fiji. Crosses: Fiji.

include the littoral zone, savannah, monsoon forest, and "open" rain forest. Stage-I species also occur in a significantly wider range of major habitats. In a later section (p. 186) it will be shown that in comparison with members of endemic Melanesian genera and subgenera, the Stage-I species *as a group*

FIGURE 7. The relation of frequency of Stage-I species to size of the genus on New Guinea. The frequency of all genera combined in each size class is given, along with the 95 per cent confidence limits. The subfamilies included are the Ponerinae, Cerapachyinae, and Myrmicinae.

show greater latitude in nest-site choice and colony size. It is further the author's subjective impression, based on too few data to analyze quantitatively, that *individual* Stage-I species show relatively wide latitude in next-site choice, but not in colony size.

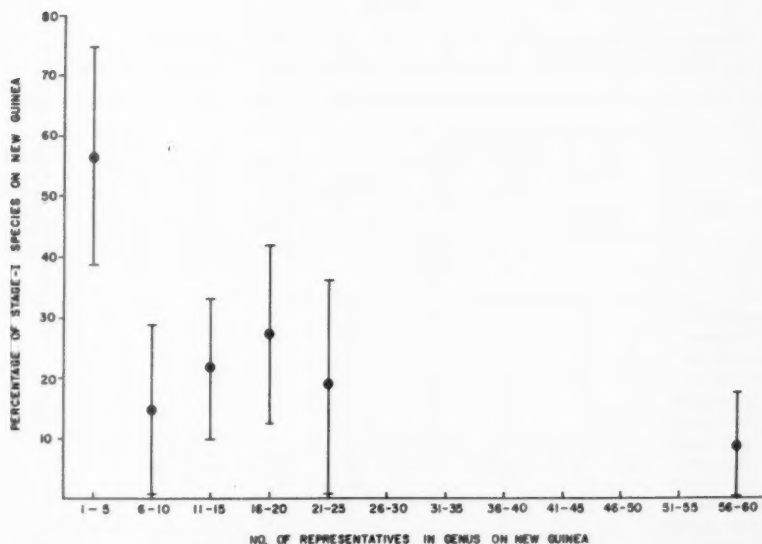It would be of interest now to inquire further into the conditions under which expanding species originate and spread. A valuable new clue is provided by the fact that a negative correlation exists between the size of the genus and the percentage of Stage-I species in the genus. As shown in figure 7, genera containing less than six species have a significantly higher percentage, about 58 per cent, of Stage-I species. Moreover, the number of Stage-I species that a single genus contains at the present time is correlated with the size of the genus but approaches a strict limit. As shown in table 3 and figure 8, even the largest genera (Pheidole, Crematogaster, Strumigenys, Odontomachus) have been able to generate no more than three Asia-based Stage-I species or four New Guinea-based ones. Further, there is a limit to the number of Stage-I species of any genus that coexist on a single island. On the largest of the Melanesian islands, New Guinea, only the dolichoderine genus Iridomyrmex has as many as seven Stage-I representatives. Iridomyrmex is exceptional in being Australia-based and in having Stage-I species conspicuously successful around human settlements. The largest ponerine and myrmicine genera have no more than five Stage-I representatives on New Guinea.

TABLE 3

Some faunal characteristics of ponerine, cerapachyine, myrmicine, and dolicho-
derine genera occurring in tropical Asia and Melanesia. Further explanation in
the text.

Genus	No. of species in central tropical Asia	No. of species originating in central tropical Asia	No. of Stage-I species originating in central tropical Asia	No. of species in New Guinea	No. of species originating in New Guinea	No. of Stage-I species originating in New Guinea	No. of Stage-I species present on New Guinea from all sources	Presence of endemics in other faunal regions
Amblyopone	7	7	0	1	0	0	1	+
Prionopelta	1	1	1	2	2	1	1	+
Myopopone	1	1	1	1	0	0	1	−
Mystrium	1	1	1	1	0	0	1	+
Rhytidoponera	0	0	0	12	12	1	1	+
Gnamptogenys	12	12	0	6	6	0	0	+
Proceratium	2	2	0	1	1	0	0	+
Discothyrea	2	2	0	1	1	1	1	+
Leptogenys	25	25	2	13	12	1	3	+
Anochetus	21	21	1	6	5	1	2	+
Odontomachus	8	8	2	17	14	3	5	+
Platythyrea	7	7	1	2	1	0	1	+
Bothroponera	19	19	1	2	?	?	?	+
Ectomomyrmex	13	13	0	6	6	1	1	−
Centromyrmex	1	1	0	0	0	0	0	+
Cryptopone	2	2	2	4	2	1	3	+
Diacamma	11	11	1	1	0	0	1	−
Emeryopone	1	1	0	0	0	0	0	−
Brachyponera	4	4	1	2	1	1	2	+
Mesoponera	2	2	0	2	2	1	1	+
Trachymesopus	4	4	2	3	1	1	3	+
Ponera	30	30	2	20	18	3	5	+
Pseudoponera	2	2	1	0	0	0	0	−
Myopias	6	6	0	14	14	0	0	−
Harpegnathos	2	2	0	0	0	0	0	−
Odontoponera	1	1	1	0	0	0	0	−
Cerapachys	12	12	0	9	9	1	1	+
Phyracaces	5	5	0	2	2	0	0	+
Lioponera	2	2	0	1	1	0	0	−
Simopone	2	2	0	0	0	0	0	−
Sphinctomyrmex	?	?	?	?	?	?	?	+
Crematogaster	70	70	1	26	25	4	5	+
Pheidole	81	81	2	58	56	4	5	+
Strumigenys	16	16	1	21	20	3	4	+
Hypoclinea	20	20	1	1	0	0	1	+
Monoceratoclinea	0	0	0	2	2	0	0	−
Leptomyrmex	0	0	0	3	3	1	1	+
Technomyrmex	10	10	1	2	1	0	1	+
Turneria	1	?	?	3	3	1	1	−
Iridomyrmex	1	0	0	13	8	2	7	+

In seeking an explanation for this phenomenon, we may look directly to
the role of interspecific competition. There is excellent additional evidence
to favor the hypothesis that competition is decisive. The Stage-I species
on New Guinea include no closely related pairs. Stage-I species in the same
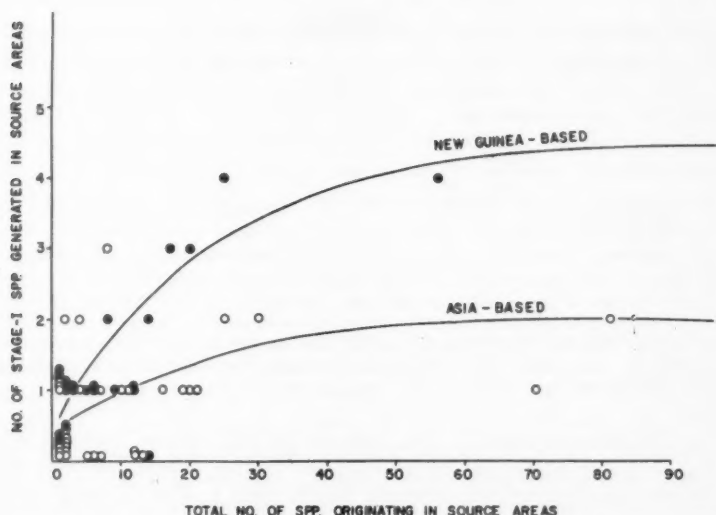
FIGURE 8. The relation of size of genus to number of contained Stage-I species in the Ponerinae, Cerapachyinae, and Myrmicinae in Asia (open circles) and in New Guinea (closed circles). Note that no genus has been able to generate more than four Stage-I species from one source area. See also table 3 and further explanation in the text.

genus tend to be markedly different from one another in morphology, ecology, and behavior. In most cases where the same broad species group is represented·by more than one Stage-I member, for example, *Odontomachus simillimus* with *O. cephalotes*, *O. malignus* with *O. saevissimus*, the members occur in different major habitats. Additional supporting evidence is found in the phenomenon of *ecological release*: although the Stage-I species tend to be restricted to marginal habitats on New Guinea and Fiji, which have large endemic faunas, they are not so restricted in the more depauperate Solomon Islands and New Hebrides. On Espiritu Santo, where the author conducted field studies, several Stage-I species, for example, *Odontomachus simillimus*, *Pheidole oceanica*, *P. sexspinosa*, *P. umbonata*, were among the dominant ant species in deep virgin rain forest. At lowland stations on New Guinea, the same species were much sparser and limited to marginal habitats. Other Stage-I species that have marginal distributions on New Guinea, including *Rhytidoponera araneoides*, *Iridomyrmex cordatus*, and *Oecophylla smaragdina*, are dominant in the rain forests of the Solomon Islands (Mann, 1919). There can be no question that interspecific exclusion underlies this phenomenon. Suitable nesting sites and trophophoric fields are virtually saturated with ant colonies in both New Guinea and outer Melanesia. Where large native faunas exist, there is literally no room for significant populations of Stage-I species. Reference has already been made to the role of direct colony conflict in interspecific exclusion of Stage-I ant introduced spe-

TABLE 4

Asia-based genera					New Guinea-based genera				
		Represented in other faunal regions					Represented in other faunal regions		
		+	−				+	−	
Producing Stage-I species	+	7	3		Producing Stage-I species	+	10	0	
	−	17	28			−	12	10	

Classification of the smaller ant genera (1–5 species in the Oriental-Melanesian region) according to whether Stage-I species are produced (+) or not (−) and whether other member species occur in other faunal regions (+) or not (−). All subfamilies are included. Only three of the ant genera limited to the Oriental-Melanesian region produce Stage-I species within it. Further explanation in text.

cies in the Solomon Islands. This may be but one form of competition that produces the displacement-release effect. (Other modes of competition among ant species are discussed by Brian, 1952.) The existing zoogeographic evidence indicates that ecological release is a secondary phenomenon, appearing when initially displaced, expanding species reach depauperate archipelagoes.

Expanding species are able to cross water gaps effectively and colonize empty islands with startling ease. By 1921, less than 40 years after its denudation, the island of Krakatau had been colonized by the four ponerine species, *Odontoponera transversa*, *Ponera confinis*, *Brachyponera luteipes*, and *Odontomachus simillimus* (Wheeler, 1924). *Brachyponera luteipes* had been established by no later than 1909 (Forel, 1909). By 1933 an additional species, *Anochetus graeffei*, was established and a sixth species, *Myopias breviloba*, was known from winged queens (Wheeler, 1937). These six species are among the most widespread of the native Oriental ponerine ants. Together they make a fauna approximately the same size as those found on islands of comparable area in the Moluccas and Melanesia. Similar rapid colonization to near-saturation level occurred on the "empty" islands of Verlaten and Sebesi, near Krakatau.

Finally, the genera and subgenera that have produced Stage-I species are in the great majority represented by distinct species in other faunal regions. This marked characteristic is illustrated in table 4. Expressed another way, taxa now generating Stage-I species in the Oriental-Melanesian region have usually had a record of success in other parts of the world. And, conversely, taxa that are confined to this region are seldom able to generate Stage-I species within it.

BIOLOGICAL CHARACTERISTICS OF AUTOCHTHONOUS AND RETREATING TAXA

Certain ant genera and subgenera are either endemic to Melanesia or clearly contracting within it, that is, centered in Melanesia and represented elsewhere by scattered relict endemics. These include Adelomyrmex s. str.,

Adelomyrmex (Arctomyrmex), Aphaenogaster (Planimyrma), Ancyridris, Da-
cetinops, Arnoldidris, Archaeomyrmex, Willowsiella, Poecilomyrma, Cre-
matogaster (Rhachiocrema), Crematogaster (Xiphocrema), Pheidole (Electro-
pheidole), Pheidole (Pheidolacanthinus), Monoceratoclinea, Mesoxena,
Camponotus (Myrmegonia), Camponotus (Condylomyrma), Polyrhachis (Doli-
chorhachis). Endemic Melanesian taxa generally contain a relatively small
number of species limited to one of the three following archipelagoes: New
Guinea, Solomons, and Fiji. It is not possible to determine whether they
are relicts or autochthonous taxa at maximum range. (New Caledonia, which
has a virtually independent ant fauna derived from Australia, is not con-
sidered here.)

In contrast with the above set of taxa are genera and subgenera, head-
quartered in tropical Asia or tropical Asia plus New Guinea, which are gen-
erating Stage-I species and are not notably disjunct. These include Aenic-
tus, Mystrium, Leptogenys, Anochetus, Odontomachus, Platythyrea, Crypto-
pone, Diacamma, Brachyponera, Trachymesopus, Ponera, Pseudoponera,
Odontoponera, Cardiocondyla, Crematogaster (Orthocrema), Strumigenys,
Rhopalomastix, Calyptomyrmex, Pheidole s. str., Pheidologeton, Monomo-
rium, Vollenhovia, Tetramorium, Hypoclinea, Technomyrmex, Pseudolasius,
Paratrechina (Nylanderia), Oecophylla, Camponotus (Dinomyrmex), Campono-
tus (Myrmamblys), Camponotus (Colobopsis), Camponotus (Tanaemyrmex),
Polyrhachis (Polyrhachis), Polyrhachis (Chariomyrma), Polyrhachis (Myrma),
Polyrhachis (Myrmhopla).
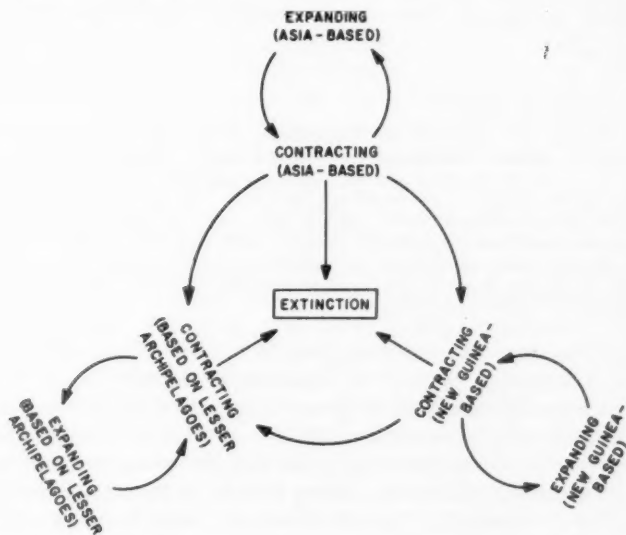
FIGURE 9. The taxon cycle in Melanesian ants. The following features are pos-
tulated: the taxon can undergo alternate expansion and contraction, with or without
speciation, for an indefinite period of time; it can shift its headquarters from a large
land mass to a smaller one but not in the opposite direction.

For convenience, the relative evolutionary positions of the two sets of taxa can be classified as "contracting" and "expanding" in the simple dichotomy represented in figure 9. Taxa endemic to the Solomons or Fiji can be safely regarded as either contracting or at least permanently confined, according to the evidence previously discussed. Taxa endemic to or centered on New Guinea with relicts outside may either be retreating or potent, that is, destined to expand; it is not feasible to speculate further on this

TABLE 5

Characteristic	Expanding taxa			Receding or autoch- thonous taxa			χ^2	P	χ_c^2*	P_c*	Statistical interpretation
	+++	++	+	+++	++	+					
Spinescence	3	33	1	12	5	1	20.93	< 0.0001	18.04	< 0.0001	Highly significant
Cryptobiosis of non-spinescent forms	5	...	26	3	...	2	3.99	0.04	2.59	0.10	Doubtfully significant
Colony size	3	10	3	0	2	4	6.70	0.01	4.14	0.04	Significant
Terricolous species: small log nest site	5	...	18	4	...	1	6.40	0.01	4.00	0.04	Significant
Prominent use of odor trails	10	...	16	0	...	8	4.36	0.04	2.70	0.10	Doubtfully significant
Species limited chiefly to the mid-mountain rain forests	1	...	31	6	...	6	12.04	< 0.001	9.29	< 0.001	Highly significant
Species limited entirely to inner rain forest habi- tats	7	...	23	13	...	2	16.25	< 0.001	14.01	< 0.001	Highly significant

* Yates—corrected for continuity.

Some biological differences between expanding genera and confined (retreating or autochthonous) genera in Melanesia. Each qualitative characteristic has been classified as present (+++) or absent (+). Continuously varying characteristics have been roughly classified quantitatively into three classes. Colony size is based on estimates given in Wilson (1959d) and is partitioned into three groups with adult populations of 90 or less (+), 100–800 (++), or 1000 or greater (+++). Not all taxa were well enough known to classify with respect to each characteristic. Only characteristics are shown in which these differences between the two sets of taxa are significant at the 95 per cent confidence level.

distinction. In any case, it is clear that the two sets of taxa belong to different major stages in cyclical evolutionary development in the Oriental-Melanesian fauna (Wilson, 1959a). We may now raise the following question: do taxa undergo parallel biological changes correlated with these zoogeographic episodes? To explore this possibility, the two groups of taxa were scanned for biological differences among diverse morphological, ecological, and behavioral characters. Certain differences were found, as shown in table 5. Background information concerning most of these characters, apart from their evolutionary classification, has already been presented in earlier papers (Wilson 1959a, b).

DISCUSSION: A THEORY OF THE TAXON CYCLE

Enough zoogeographic and ecological data have now been accumulated to justify a preliminary reconstruction of the generalized taxon cycle of the Melanesian ant fauna. Let us start with the actual process of speciation. The evidence suggests that the chief geographic barriers are the water gaps. Speciation probably occurs by internal fragmentation of some populations on the great island of New Guinea, but this appears to be a minor phenomenon, principally involving retreating endemic species. As a rule, semispecies and superspecies, comprising the populations at the threshold of speciation, break at the water gaps. Furthermore, the wider the water gaps, the more frequent the breaks between the allopatric populations. Finally, accumulations of related species on single archipelagoes or islands is chiefly the result of multiple invasions (Wilson, 1959a).

Expanding species in Melanesia originate almost entirely from tropical Asia, New Guinea, and Australia. These are moreover the "potent" species that must from time to time give rise to new taxa. However, the fossil record reveals that ant evolution has been relatively conservative since the early Tertiary (Wheeler, 1914; Carpenter, 1931). The zoogeographic evidence indicates that the origin of new potent taxa of higher rank is a rare event in tropical Asia and Melanesia. Among the 41 smaller ant genera confined to tropical Asia and New Guinea, only three (Myopopone, Odontoponera, Pseudoponera) contain expanding species. Of 51 ant genera of comparable representation in tropical Asia and New Guinea but with representation in other faunal regions (hence, older genera?), 17 contain expanding species. (See table 3.) Other distinctive endemic genera have been evolved in the Solomons, Fiji, and New Caledonia but are strictly limited in size and show no sign of extending their ranges. Thus, the origination of higher taxa is a relatively common event in the Oriental-Melanesian region, but the new products are usually strictly limited to the archipelagoes in which they are born. The combined evidence indicates strongly that the creation of the occasional potent new genera and higher taxa is confined to the large source areas of tropical Asia and New Guinea. Indeed, since Myopopone, Odontoponera, and Pseudoponera are all Asia-based, it is possible that tropical Asia alone serves as a significant source area of potent taxa higher than the species group. Retreating taxa can shift their headquarters from larger to smaller land masses but not in the opposite direction (figure 9).

At lower taxonomic levels, the ants seem to conform to the rule expressed earlier by Darlington (1957, 1959) for vertebrates, that dominant taxa tend to arise in and spread from the largest favorable land masses. It is possible to go a step further and specify that in Oriental-Melanesian ants, the degree of faunal interpenetration is closely correlated with land mass and only secondarily correlated with faunal size, as shown in figure 4.

There is good reason therefore to focus special attention on the ecology of the large land masses generating Stage-I species: tropical Asia and New Guinea. From our somewhat more advanced knowledge of the New Guinea

fauna, the following generalization can safely be made. Stage-I species are being produced under conditions of intense and complex competition. As a prelude to expansion out of New Guinea, they became adapted to a wide variety of marginal habitats, containing sparse ant faunas. They are excluded for the most part from the rich inner rain forest habitats by variable numbers of endemic species ecologically similar to them. The endemic competitors are characterized by a high degree of specialization correlated with a more complex partitioning of the environment (Wilson, 1959d) and by smaller individual populations. On other Melanesian islands with depauperate endemic faunas, Stage-I species penetrate the inner forest, mount dense populations there, and fill the available nesting sites.

From the evidence concerning ecological release, the following general prediction can be made: the ecological amplitude of both expanding and endemic species should be negatively correlated with the size of the island on which they occur and hence with the size of the local fauna to which they belong. This prediction cannot be rigorously tested at the present time, but it does seem to be supported by some additional evidence concerning increased variation in morphology of Fijian Ponera (Wilson, 1958a, p. 344) and in feeding habits of Fijian Strumigenys (Brown and Wilson, 1959, p. 289).

Species centered in the marginal habitats of New Guinea have greater opportunities for dispersal. They are poised along the coast and river banks which are the best points of departure for neighboring islands. The smaller corridor islands that can be used as stepping-stones possess the same simplified environments, both physical and biotic, that characterize the marginal habitats on New Guinea.

As the island stepping-stones decrease in size, the percentage of Stage-I species in their faunas increase (figure 6). All of the islands of the Sunda-Melanesian arc, with the possible exception of Fiji, support a strong complement of Stage-I species. On small and medium islands there is therefore a significant constriction of older faunal elements (figure 5). It can be deduced that since the number of Stage-I species does not vary greatly according to islands, the turnover of Stage-I species will probably not vary greatly either. But since the number of older (Stage II and III) species decreases markedly with decrease in island area, we can expect Stage-I species to replace them faster on smaller islands. This prediction seems to be verified by the pattern of distributions of disjunct species groups in Melanesia. As a rule, disjunction involving a hiatus of one or more archipelagoes occurs only after the refugium populations have diverged to species level. This is best interpreted as a result of the fact that speciation ordinarily occurs as the taxon retreats into the inner forest habitats, evidently under displacement pressure from Stage-I species (Wilson, 1959a). Taxa disappear first from the smaller islands and then, apparently progressively, from larger islands. The oldest and most divergent members of disjunct taxa are concentrated as relicts on the largest islands, for example, on New Guinea, the larger Solomons, and Viti Levu. Within the hiatuses the disjunct taxa are commonly represented by ecological vicars from other taxa which are con-

spicuously abundant and widespread ("ecologically released" species). The following example is unusually clear-cut. Several Iridomyrmex species utilize rubiaceous ant-plants of the genera Myrmecodia and Hydnophytum as their chief nesting sites. On New Guinea these plants are occupied primarily by *I. cordatus* in the marginal habitats and by *I. scrutator* in the inner forest. The ant-plants are saturated by ant colonies and the replacement is therefore virtually absolute. In the Solomon Islands *scrutator* is absent, and *cordatus* is abundant in both marginal habitats and the inner forest. On Fiji *cordatus* is absent, and the ant-plants are occupied by a third species, *nagasau*, which is closely related to *scrutator* and presumably cognate with it.

In summary, expanding (Stage-I) species in Melanesia originate almost entirely from tropical Asia, New Guinea, and Australia. Consequently, these land masses have probably been the ultimate source of all new taxa generated in the Indo-Australian Region and the immediate source of all potent new taxa. The Stage-I species evidently serve an important additional role in displacing, fragmenting, and directing the evolution of older resident species. It can be added that the taxon cycle dates no further back than the early Tertiary, when the radiation of modern ant genera began. Throughout the Cenozoic Melanesia has been broken into numerous islands, at least intermittently (Umbgrove, 1949; Derrick, 1951; Grover, 1955), thus facilitating speciation by multiple invasions. In Miocene times, the Solomon and Fiji Islands were mostly submerged. The evolution of the modern ant fauna of these islands may not date beyond this epoch. The Fijian fauna especially has a modern cast, with no indisputably ancient representatives among its endemic taxa.

A major attribute of evolutionary success in taxa is seen to be the ability to move member species into marginal habitats, at least temporarily. By examining the expanding species we might hope to discover other biological attributes that provide success, in other words, to define new biological rules that apply to the phenomenon of "general adaptation" (Darlington, 1959). Beyond generating marginal-habitat species, however, the expanding taxa appear to be distinguished by only one other common characteristic: great diversity among themselves. In fact, as noted already, one ecologically divergent elements are able to travel through the marginal-habitat channel simultaneously. From this evidence it would seem logical to conclude that general adaptation involves the acquisition of a marked ecological difference. Perhaps the larger this difference the more successful will be the taxon. But of course complete and permanent escape from the faunal equation is impossible and replacement must be inevitable, starting on the smaller islands and in the poorer habitats. Therefore, a second common quality of general adaptation is undoubtedly the ability to replace competitors in the zones of ecological overlap. Perhaps the two qualities are related as follows: the penetration of a new major niche provides the ancestral species with an unmolested population reservoir that allows it, at least for a time, to mount sufficient populations and new adaptations to usurp other niches already occupied by competitor taxa.

The endemic higher taxa, including both confined autochthons and retreating relicts, show more biological uniformity than the expanding taxa, as indicated in table 5. Individually they occur in fewer major habitats (see Wilson, 1959a, p. 137) and occupy a smaller range of nest sites. Collectively they can be characterized by other biological features that are highly variable in expanding taxa. It must be asked whether the collective features are not purely accidental, that is, random correlations derived from the scanning of a great many independent characteristics, or whether they represent a coadaptive complex correlated in some way with the declining position of the taxa in the faunal balance. In fact, most of the features do seem to be associated with the restriction of the endemic taxa to the inner forest habitat. Spinescence may not be part of the coadaptive system; this character is found in terricolous ants that forage above ground and probably serves as a protection against predators (Wilson, 1959d). It may be significant that most of the non-spinescent endemic taxa are notably cryptobiotic, that is, confined in foraging to soil cover and rotting wood. There is a strong tendency for the terricolous species to nest in small rotting logs and branches in the leaf litter; this is the preferred nest site of inner rain forest ant species generally. Colonies are relatively small, a trait closely associated with the restricting nature of the small-log nest site. Finally, odor trails are seldom if ever used, a negative characteristic generally associated with small colony size in ant species. Thus, it appears that endemic taxa are concentrated in and largely restricted to the habitats and nest sites where the greatest number of Melanesian ant species occur. The restriction is reflected in certain other adaptive characters.

If the taxon cycle described here is true for Melanesian ants, it is not necessarily true for other kinds of organisms. Ants are peculiar in several important respects: they are social, highly territorial, and so abundant as to play major roles in the ecosystems in which they live (Branner, 1912; Sernander, 1906; Tevis, 1958). As a result interspecific competition may be more important in their evolution than it is in most other groups of organisms. If the origination of potent new taxa of ants is limited to the larger land masses, this is not necessarily the case in birds (Mayr, 1954), Drosophila (Carson, 1955), or morabine grasshoppers (White, 1959). Indeed, the entire form of the taxon cycle may be altered in groups with markedly different ecology and population structure. It is one of the tasks of comparative zoogeography to determine the extent of this variation in histories.

SUMMARY

Undisturbed ant faunas of islands in the Moluccas-Melanesian arc are for the most part "saturated," that is, approach a size that is correlated closely with the land mass of the island but only weakly with its geographic location (figure 1). In the Ponerinae and Cerapachyinae combined the saturation level can be expressed approximately as $F = 3A^{0.6}$, where F is the number of species in the fauna and A the area of the island in square miles.

Interspecific competition, involving some degree of colonial warfare, plays a major role in the determination of the saturation curve. It deploys the distribution of some ant species into mosaic patterns and increases the diversification of local faunas. Perhaps because of the complex nature of the Melanesian fauna, differences between local faunas appear that give the subjective impression of randomness. Despite the action of species exclusion, the size of local faunas occurring within a set sample area increases with the total size of the island (figure 2).

Water gaps break populations and initiate speciation in Melanesia. Endemic insular faunas build up primarily by the process of multiple invasion.

Expanding species now on Melanesia originated almost exclusively from tropical Asia, New Guinea, and Australia. Faunal dominance, measured by the degree of faunal interpenetration, is a direct function of land area and is less directly related to insular faunal size (figure 4). Taxa originating in Melanesia exclusive of New Guinea are almost all confined to the archipelagoes of their birth.

The following taxon cycle is postulated. A taxon maintains its headquarters in a given land mass indefinitely, expanding and contracting cyclically, or else it declines to extinction. The headquarters can be shifted from a larger to a smaller land mass (for example, from New Guinea to Fiji) but not in the reverse direction (figure 9). Taxa originating in Melanesia exclusive of New Guinea are almost all confined to the archipelagoes of their birth.

On New Guinea, expanding species occur primarily in marginal habitats. In the inner rain forest habitats they are replaced by the large endemic faunas. On archipelagoes with small endemic faunas, the expanding species are ecologically "released," becoming abundant in the inner forest habitats and otherwise increasing their ecological amplitude. As a group they are characterized by great diversification among themselves. No genus among those studied has produced more than three Asia-based or four New Guinea-based Stage-I species (figure 8). No genus studied, including the largest and most successful, has a total of more than seven Stage-I species on New Guinea. Sympatric Stage-I species in the same genus tend to be ecologically and morphologically very dissimilar.

The following rule is predicted: the ecological amplitude of individual species, both expanding and endemic, should be negatively correlated with the size of the local fauna to which they belong and hence the size of the island on which they occur. The prediction is based on the phenomenon of ecological release of Stage-I species and appears to be supported by some fragmentary evidence relating to Fijian endemic species.

Expanding species evidently play a major role in the fragmentation and speciation of older taxa. By dominating the faunas of smaller islands they maintain hiatuses in the ranges of the disjunct taxa. By saturating the marginal habitats they restrict the older taxa to the inner rain forest.

Autochthonous and retreating taxa show certain common biological char-

acteristics coadaptive with restriction to the inner forest habitats. These involve nest site preference, colony size, and foraging behavior (table 5).

Three general attributes of success are recognized in the expanding Melanesian ant taxa: the acquisition of a significant ecological difference, which presumably reduces interspecific competition, the ability to penetrate the marginal habitats, and the ability to disperse across water gaps. It is suggested that the attributes are causally related in the sequence given. Success in the marginal habitats gives expanding species the advantage needed to encompass and progressively replace older resident taxa.

LITERATURE CITED

Branner, J. C., 1912, Geologic work of ants in tropical America. Pp. 303–333. Smithsonian Institution Report for 1911.

Brian, M. V., 1952, Interaction between ant colonies at an artificial nest-site. Entomol. Monthly Mag. 88: 84–98.

1955, Food collection by a Scottish ant community. J. Animal Ecol. 24: 336–351.

1956, Segregation of species of the ant genus *Myrmica.* J. Animal Ecol. 25: 319–337.

1956 (1958), Interaction between ant populations. Proc. Xth Intern. Congr. Entomol. 2: 781–783.

Brown, E. S., 1959, Immature nutfall of coconuts in the Solomon Islands. II. Changes in ant populations and their relation to vegetation. Bull. Entomol. Research 50: 523–558.

Brown, W. L., 1958, Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini. Bull. Mus. Comp. Zool. Harvard 118: 175–362.

1960, Contributions.... III. Tribe Amblyoponini. Bull. Mus. Comp. Zool. Harvard 122: 145–230.

Brown, W. L., and E. O. Wilson, 1959, The evolution of the dacetine ants. Quart. Rev. Biol. 34: 278–294.

Carpenter, F. M., 1930, The fossil ants of North America. Bull. Mus. Comp. Zool. Harvard 70: 3–66.

Carson, H. L., 1955, The genetic characteristics of marginal populations of Drosophila. Cold Spring Harbor Symp. Quant. Biol. 20: 276–287.

Chapman, J. W., and S. R. Capco, 1951, Check list of the ants (Hymenoptera: Formicidae) of Asia. Mon. Inst. Sci. Technol. (Manila, P. I.) 1: 1–327.

Darlington, P. J., 1957, Zoogeography. John Wiley & Sons, Inc., New York, N. Y.

1959, Area, climate and evolution. Evolution 13: 488–510.

Derrick, R. A., 1951, The Fiji Islands. 334 pp. Gov. Printing Dept., Suva, Fiji Islands.

Forel, A., 1909, Ameisen aus Java und Krakatau beobachtet und gesammelt von Herrn E. Jacobson. Notes Leyden Mus. 31: 221-232.

Grover, J. C., 1955, Geology, mineral deposits, and prospects of mining development in the British Solomon Islands Protectorate. Mem. Interim Geol. Surv. Brit. Sol. Is. 1: 1-149.

Mann, W. M., 1919, The ants of the British Solomon Islands. Bull. Mus. Comp. Zool. Harvard 63: 273-391.

   1921, The ants of the Fiji Islands. Bull. Mus. Comp. Zool. Harvard 64: 401-499.

Mayr, E., 1954, Change of genetic environment and evolution. *In* Evolution as a process, ed. by J. Huxley *et al.* Pp. 157-180. George Allen & Unwin Ltd., London, England.

Sernander, R., 1906, Entwurf einer Monographie der europäischen Myrmekochoren. 410 pp. Uppsala.

Tevis, L., 1958, Interrelations between the Harvester Ant *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39: 695-704.

Umbgove, J. H., 1949, Structural history of the East Indies. 63 pp. Cambridge Univ. Press, Cambridge, England.

Wheeler, W. M., 1914, The ants of the Baltic amber. Schrift. Physik. Öken. Ges. Königsberg 55: 1-142.

   1924, Ants of Krakatau and other islands in the Sunda Strait. Treubia 5: 1-20.

   1937, Additions to the ant-fauna of Krakatau and Verlaten Island. Treubia 16: 21-24.

White, M. J. D., 1959, Speciation in animals. Austral. J. Sci. 22: 32-39.

Wilson, E. O., 1957, The *tenuis* and *selenophora* groups of the ant genus *Ponera* Bull. Mus. Comp. Zool. Harvard 116: 355-386.

   1958a, Studies on the ant fauna of Melanesia, I-IV. Bull. Mus. Comp. Zool. Harvard 118: 101-153, 303-371.

   1958b, Patchy distributions of ant species in New Guinea rain forests. Psyche 65: 26-38.

   1959a, Adaptive shift and dispersal in a tropical ant fauna. Evolution 13: 122-144.

   1959b, Studies on the ant fauna of Melanesia, V. Bull. Mus. Comp. Zool. Harvard 120: 483-510.

   1959c, Studies on the ant fauna of Melanesia, VI. Pacific Insects 1: 39-57.

   1959d, Some ecological characteristics of ants in New Guinea rain forests. Ecology 40: 437-447.

Wilson, E. O., and R. W. Taylor, 1961, The ants of Polynesia. (ms.)

POPULATION EFFECTS OF NATURAL SELECTION*

ROBERT H. MACARTHUR

Division of Biology, University of Pennsylvania,
Philadelphia, Pennsylvania

This paper has two themes. The first is that the traditional approach to population ecology, via the fluctuation and interaction of species populations, is about the hardest possible. The second is that where natural selection proceeds along an unambiguous course, it controls population processes in a simple, readily understandable, way. The remarkably precise convergence of unrelated forms whose activities are similar shows how nice is the control exercized by selection over phenotype.

The central difficulty in understanding populations as an outcome of natural selection arises from the fact that the good of the species is not always equivalent to the good of the individual genotype, and conversely. There is plenty of direct evidence that more fit genotypes replace less fit, and there is plenty of circumstantial evidence (mostly from the fossil record) that more fit species replace less fit. But the relative magnitudes of these processes and the equilibrium they reach are unknown and hence controversial. Only when what is good for the species coincides with what is good for the genotype is it easy to understand the population effects of natural selection. In what follows a collection of examples is presented, in no particular order, and with no pretense of reviewing the literature. The very nature of the predictions made requires that we consider fairly orderly populations. It seems much harder to make interesting predictions about the more erratic populations which are more appropriately treated by the methods of Andrewartha and Birch (1954). See also Birch (1960).

SEX RATIO

One of the most impressive examples of an understanding reached by applying knowledge of natural selection is Fisher's (1958) theory of sex ratio, proposed in 1930 and further discussed by Kolman (1960) and Bodmer and Edwards (1960). When every individual has a parent of each sex, the group of all males must contribute (except for sex chromosomes) the same as the group of all females to the genetic ancestry of future generations. Then, other things being equal, whichever sex is present in short supply has greater value *per individual* and hence is favored by natural selection. This accounts for an approximately equal frequency of males and females. More

generally, males and females are not always equally easy to rear, and, to achieve the greatest fitness parents should have a biased sex ratio. Finally, an X-chromosome trait which results in excess production of females will be represented in more of the next generation than will its allele, so that the theory doesn't apply to sex-linked genes. However, any autosomal gene suppressing such a trait will, of course, be favored so that, because of the large number of autosomes, sex ratio determination may tend to become auto-somal, leaving the first theory correct.

BIRTH RATE, DEATH RATE, AND GEOGRAPHIC DISTRIBUTION

Lack (1957) has suggested that birth rate is adjusted to the largest value the parents can successfully rear to reproducing age. When there is no pa-rental care, the limits are set by the total volume of eggs the female can lay, but their size and number may be adjusted (Hutchinson, 1951). Slobod-kin and Richman (1956) have listed some reasonable exceptions which don't, however, affect the validity of the argument. This leaves largely unex-plained the puzzling correlation between clutch size and the magnitude of inevitable hazards to which a bird is subject. Lack (1949) suggests that birds generally lay larger clutches in high latitudes not because mortality is greater there, but because high latitude food and day length make possible larger clutches. Without rejecting this argument, a different viewpoint gives considerable extra insight. Consider, instead, the natural selection of a species' distribution. Briefly, a species will only settle where its birth rate exceeds its inevitable mortality. And if, due to severe climate and the hazards of longer migration, mortality is always greater at high latitudes, then so must clutch size be higher, or the species won't live there. More precisely, birth rate and death rate are both functions of latitude (say) and population density. The species will, by natural selection, choose that geo-graphic distribution for which zero-density birth rate exceeds zero-density death rate and then at each such place will increase in population density until the births and deaths balance. (A zero-density birth rate is, of course, the limit of the birth rate as population density approaches zero.) This argu-ment does not necessarily predict an ever increasing birth rate as we pro-ceed to higher latitudes. But it does make this a likely tendency and also explains the high clutch sizes observed on mountains (Johnston, 1954). There is virtually no direct evidence bearing on this theory. A corollary for which there is supporting evidence (Mayr, 1946; MacArthur, 1959) is that mi-grants will settle in greatest density in places where the summer increase in food supply is greatest.

"CONVEX" ACTIVITIES

Consider an adaptation which caused a bird to feed only on one of the suitable kinds of tree in a forest. Then during the daily rounds of food gath-ering the bird would be passing through many trees in which it could not feed. Or, consider an adaptation which predisposed a bird to feed on only one kind of insect in a habitat in which many other kinds of insect of simi-

lar form and palatability were present. Then, during its daily rounds, the bird would encounter many potential food items which it could not exploit. In both of these examples, the bird is making inefficient use of its resources and wasting energy. Contrast with these a bird adapted for eating all palatable insects encountered in all kinds of trees, specialization occurring in the feeding height. Such a bird would move through the forest at the proper height, feeding more or less continuously, and normally would be more fit.

Such efficient activities may be called "convex" in the sense that, given any two activities for which the species is adapted, the species is also adapted for intermediate activities. (There is a mathematical theory of convex bodies, which is appropriate.) Feeding sites may fail to be convex (as in the first example) and the nature of acceptable food may be (as in the second example). It seems that natural selection would always favor convex foods and would normally favor convex feeding sites. Only when the advantage due to specialization to a patchy food source outweighs the disadvantage caused by the wasted activity will food sites fail to be convex. Fruit eating birds such as parrots are an obvious example. Notice that while specialization of a bird to a single tree species may not be convex, specialization of a small organism like an insect is much more likely to be. For, while a bird daily forages in many trees, a caterpillar may do all its feeding on one branch. No systematic evidence seems to have been gathered on this subject.

DIVERSITY OF SPECIES

When adjacent habitats support different numbers of species, the reason is presumably that one in some way will support more than the other, for otherwise natural selection would favor a redistribution. Why would one habitat offer greater opportunity than a second? This is best understood as follows: A single herbivore feeding on all the kinds of plant food or a single carnivore eating all the herbivores would have to be a "jack-of-all-trades," and, presumably, for this reason a "master of none." Thus an incoming, specialized species would find what is often called an "unoccupied niche" (although it is hard to see what was unoccupied) and would persist in that habitat. Further species would continue to enter as long as the increased efficiency due to specialization was not outweighed by loss of efficiency because of the non-convex activities resulting from many species. There is no evidence on whether this limit has ever been reached, but in any case, adjacent occupant's habitats should, on the average, show about equal degrees of specialization. Bearing this in mind, the number of species occupying a habitat should be proportional to some measure of the diversity of the habitat and, from what was said about convex activities, we might expect bird species diversity at a given latitude to be controlled not by plant species diversity but instead by some structural diversity of the habitat. This appears correct [MacArthur and MacArthur (in press), where it is shown that the vegetation profile of a habitat, and not the number of plant species, controls bird species diversity].

THE DIFFICULTY OF UNDERSTANDING SPECIES INTERACTIONS

A predator which "harvests" its prey so as to achieve the largest possible continued yield must prudently avoid overeating and thus reducing the prey population to such a low level that it can no longer produce at a large rate. A population composed of such predators would face a more certain future than one which dangerously reduces its food level. On the other hand, a genotype which enabled its bearer to exploit food supplies to a scarcer level would outcompete others and hence be more fit (at least in times of food shortage). Who can say, then, whether or not natural selection will normally lead to prudent harvesting of food? At least the concentration of prudent eaters must be always on the decrease and chance processes may be required for selection for prudence. But without knowledge about this it is difficult to make predictions bearing on predator-prey or competition interactions. And "limiting factors" are equally intractable. In fact the evidence suggests that nearly all factors are often "limiting" since they interact.

It is worth mentioning that there is no ambiguity about one aspect of predator behavior. For if a predator depends upon fluctuating food supplies it will surely be better off to switch its attentions to whichever food is the most available. If several food species alternate being most available, then specialization to feed on one or the other would often be harmful. Thus while prey often have one principal predator to specialize on escaping, the predators usually cannot specialize on hunting that prey.

DISCUSSION AND CONCLUSIONS

There are innumerable other questions on which this approach could be used with profit. But these are sufficient to suggest the following way of looking at ecological problems: There seems to be good evidence, for birds at least, that the combined density of individuals of all species is controlled by the amount of food available. For instance, Crowell (1961) has found that the few Bermuda species have as many combined individuals as the many mainland species, each Bermuda one occupying a wider variety of habitats (but not a wider variety of feeding activities) than that species does on the mainland where additional species are present. Now, as indicated in the last paragraph there is evidence on the number of species the habitat will support. The mean abundance of the species is then quite predictable—the total density divided by the number of species. And when adequate theories of relative abundance become available [a start has been provided, see MacArthur (1960), Hairston (1959)] then a fairly complete understanding of the equilibrium abundances of stable populations such as birds will be achieved.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch, 1954, The distribution and abundance of animals. Univ. of Chicago Press, Chicago, Ill.

Birch, L. C., 1960, The genetic factor in population ecology. Amer. Nat. 94: 5-24.

Bodmer, W. F., and A. W. F. Edwards, 1960, Natural selection and the sex ratio. Ann. Human Genet. 24: 239–244.

Crowell, L., 1961, The effect of reduced competition in birds. Proc. Natl. Acad. Sci. 47: 240–243.

Fisher, R. A., 1958, The genetical theory of natural selection. Dover Publications, New York, N. Y.

Hairston, N. G., 1959, Species abundance and community organization. Ecology 40: 404–416.

Hutchinson, G. E., 1951, Copepodology for the ornithologist. Ecology 32: 571–577.

Johnston, R. F., 1954, Variation in breeding season and clutch size in song sparrows of the Pacific coast. Condor 56: 268–273.

Kolman, W. A., 1960, The mechanism of natural selection for the sex ratio. Amer. Nat. 94: 373–378.

Lack, D., 1949, Comments on Mr. Skutch's paper on clutch size. Ibis 91: 455–458.

Lack, D., J. Gibb and D. Owen, 1957, Survival in relation to brood-size in tits. Proc. Zool. Soc. London 128: 313–326.

MacArthur, R. H., 1959, On the breeding distribution pattern of North American migrant birds. Auk 76: 318–325.

1960, On the relative abundance of species. Amer. Nat. 94: 25–36.

MacArthur, R. H., and J. W. MacArthur, 1961, On bird species diversity. Ecology (in press).

Mayr, E., 1946, History of the North American bird fauna. Wilson Bull. 58: 1–41.

Slobodkin, L. B., and S. Richman, 1956, The effect of removal of fixed percentages of the newborn on size and variability in populations of *Daphnia pulicaria* (Forbes). Limnol. Oceanog. 1: 209–237.

ADVICE TO AUTHORS

THE AMERICAN NATURALIST will welcome articles which contribute to the purposes outlined on the inside front cover.

Material intended for publication should be prepared to conform to the style in the current issues. It should be typewritten with double spacing, leaving a two inch margin at the right for editorial directions. Each table should be typed on a separate sheet. Footnotes to text statements should be avoided since they can usually be included in the text, parenthetically if necessary. Where unavoidable, they should be numbered consecutively and typed on a separate sheet, since they will be set in a different type size. Footnotes to tables are often necessary; they should be designated by asterisks, daggers and similar signs to avoid confusion with the numerals in the tables. Legends for figures should be typewritten on separate sheets.

Each article, except letters to the Editors, should contain a brief summary.

The "Literature Cited" assumes special importance in articles of the sort which THE AMERICAN NATURALIST hopes to publish. Authors are asked to give for each reference, the author or authors, the year of publication, full title and full citation, without abbreviation, of the journal, the volume number, the beginning and ending pages; or in the case of books, the edition number, the number of pages, and the name and address of the publisher. Current issues can be given as samples of the style desired. Bibliographies which do not conform to the requirements above will be returned to the authors for correction. It is understood that general addresses will often not be accompanied by bibliographies.

Reprints will be supplied when ordered at the time of return of proofs, according to the prices quoted on the order form. Reprints of "Letters to the Editors" can be furnished only as reprints of the whole section of "Letters" which may include several. Articles excessive in length or extent of detailed data, but otherwise acceptable to the Editorial Board, may be published as supplements when costs are paid by the authors.